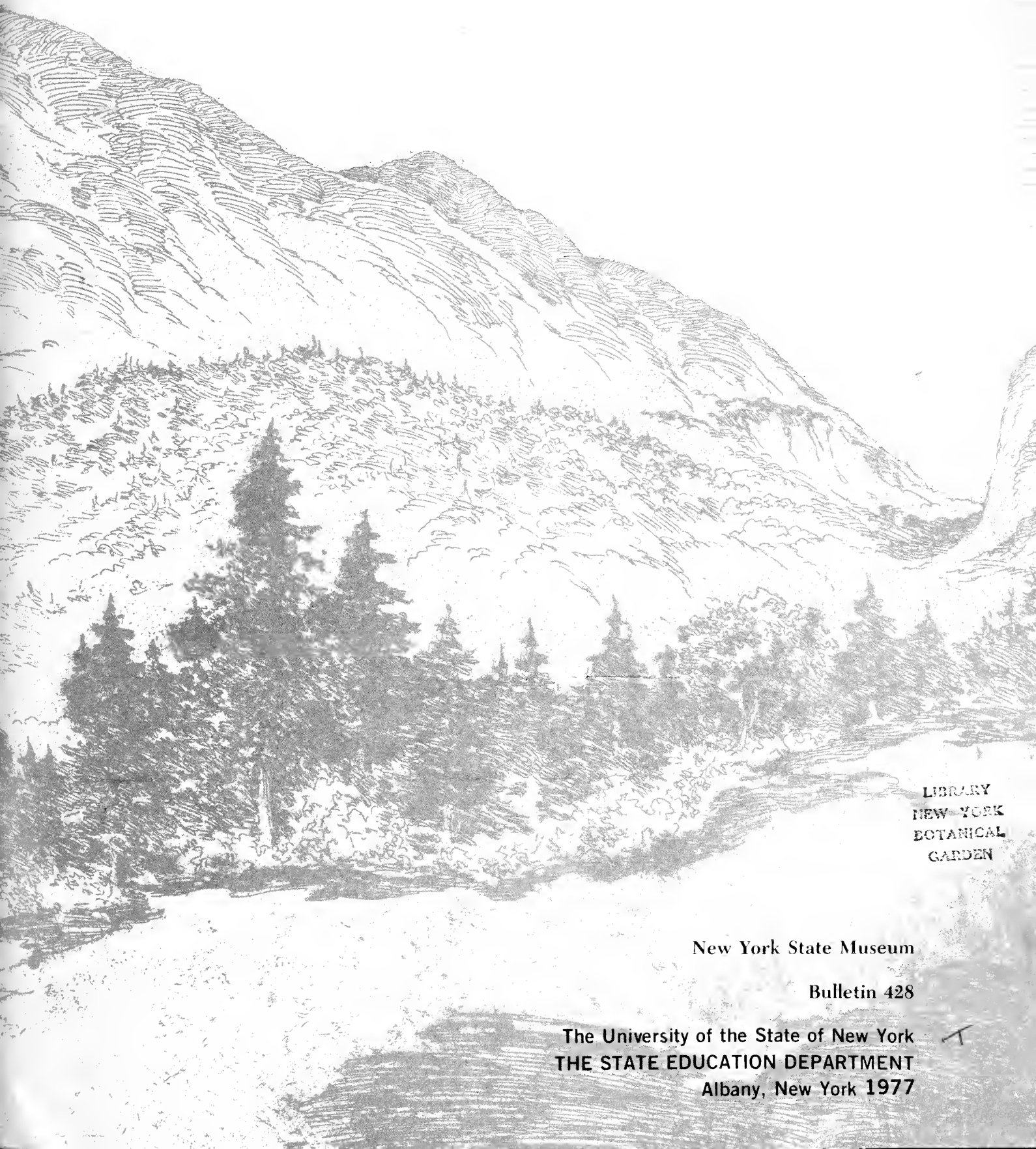


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Species Diversity and Community Structure in Bryophytes: New York State Studies

Nancy G. Slack



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Nancy G. Slack
Russell Sage College

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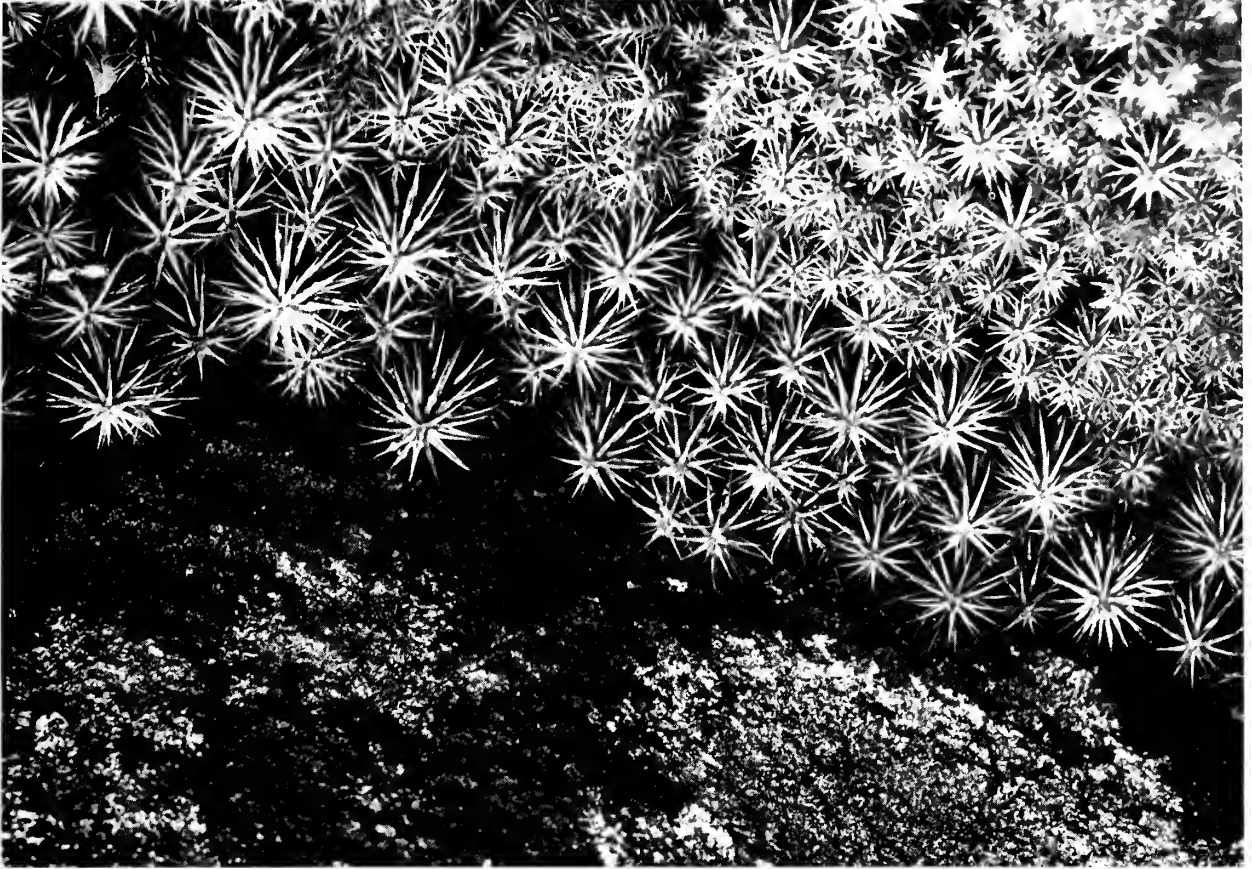
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Polytrichum juniperinum and *P. piliferum* near timberline, Whiteface Mountain.

(photo by A. B. Wellborn)

Both Forbes and Darwin realize struggle but see that it has produced harmony. Today perhaps we can see just a little more. The harmony clearly involves great diversity, and we now know . . . that every level is surprisingly diverse. We cannot say whether this is a significant property of the universe; without the model of a less diverse universe, a legitimate but fortunately unrealized alternative, we cannot understand the problem. We can, however, feel the possibility of something important here, appreciate the diversity, and learn to treat it properly.

G. Evelyn Hutchinson, 1965
in *The Ecological Theatre and the
Evolutionary Play*

Acknowledgments

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Thanks are due also to Drs. Howard Crum and Robert Ireland and to Drs. Norton Miller and S. Rob Gradstein for the verification or identification of critical mosses and hepatics, respectively. Elisabeth Manz, Edward Valentine, and Sigrin Newell provided valuable field and technical assistance. A. B. Wellborn is thanked for his excellent photography and Carl George for kindly allowing use of some of his data. The Nature Conservancy supported, in part, the research at Kenrose Preserve. The Atmospheric Science Center, SUNY, Albany, generously provided laboratory and other facilities at Whiteface Mountain.

Finally, I wish to thank Dr. Richard Monheimer of the New York State Science Service for his help in seeing the manuscript through to publication, and the Donald Richards Fund, The New York Botanical Garden, for a grant to aid in the publication of this Bulletin.

COVER: Mt. Whiteface in the Adirondack Mountains. Etching by Herbert S. Kates.

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Species Diversity and Community Structure in Bryophytes: New York State Studies

by Nancy G. Slack

Introduction

The Early Study of Bryophytes in New York State

The study of the mosses and liverworts of New York State has a long history. Collections in the New York Botanical Garden go back 150 years. During the period between 1830 and 1910, more than 40 different men and women made permanent collections of bryophytes in New York State.

Charles Horton Peck, who was the first official New York State Botanist and is now known primarily as a mycologist, did important work on bryophytes early in his career. He collected specimens in both the Adirondacks and the Helderbergs, the two areas included in this study. In 1866, he published a list of New York State bryophytes in the Nineteenth Annual report of the Regents of The University of the State of New York. This early list included 274 mosses and 66 liverworts.

Three other important bryologists also contributed to this list: Leo Lesquereux, the Hon. George W. Clinton, and Coe Finch Austin. Austin collected specimens mostly in Orange County, New York, but also near Albany, and he determined specimens for other bryologists, including Peck. He was also the first American authority on liverworts. Clinton, son of Governor DeWitt Clinton, was a judge in Buffalo, and collected mainly in western New York and around Niagara Falls. Lesquereux, who came to this country from Switzerland in 1848, was primarily a paleobotanist, the authority on the Appalachian coal flora and, as such, the first member to be elected to the newly formed National Academy of Sciences. He was also a very active bryologist who worked with William S. Sullivant in Columbus, Ohio, but collected widely in areas including the Adirondack Mountains of New York. Before 1866, he had collected on the top of Mt. Marcy, the highest Adirondack peak, as well as on Whiteface Mountain, on which most of this study was done. He corresponded with and encouraged Peck, as can be seen from the following letter, written in 1867:

Cambridge, 23 October, 1867

My dear Mr. Peck,

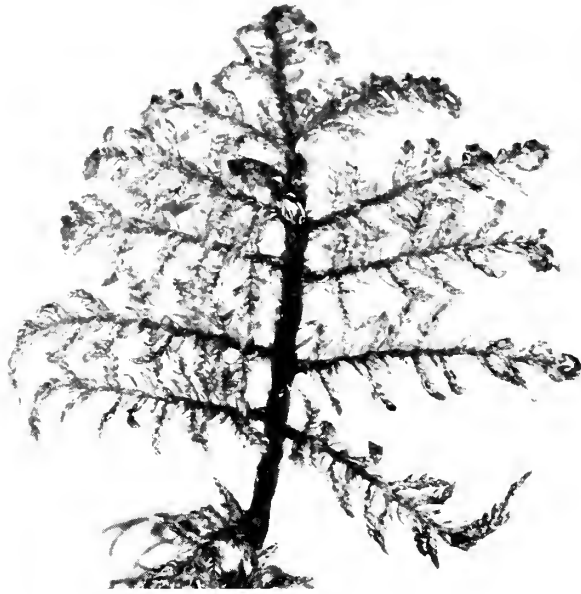
Your letter of the 5th and package of mosses was

sent to me here in Columbus. I received it today only. I shall return home about the 7th of November and will then examine your specimens and report. I was glad to hear from you again and expect some fine things from you from the Adirondack Mts. I found also some mosses especially *Orthotricha* around Placid Lake [Lake Placid] but still more at and near the top of White side [Whiteface?] Mt. and Mt. Marcy. Did you reach Mt. Marcy?

Your friend,
L. Lesquereux

These early bryologists worked almost entirely without manuals. In another letter to Peck, Lesquereux replied to a question of Peck's that no, there was not any manual to use for hepatics. Lesquereux and Thomas P. James first published a *Manual of the Mosses of North America* in 1884. There were, however, early collections of bryophytes both in Albany and New York City, and later at Cornell University in Ithaca, as well as in private collections. Many specimens were exchanged among bryologists; Austin, for example, received collections from bryologists in British Columbia, New Brunswick, South Carolina and Florida, as well as from New York State. Peck corresponded with a dozen other bryologists, and sent out many specimens.

The nineteenth-century bryologists came from a variety of professions, and many of them traveled widely. Thomas Potts was a druggist, Clinton, a judge. George Best, Elliot C. Howe, and Smith Ely Jelliffe were all physicians, as well as active bryophyte collectors in different parts of the State. William Brewer was a geologist and botanist and later professor of agriculture at Yale University. He made collections in California and Alaska as well as in New York. Orator Cook, an early collector of hepatics in New York State, was an agent for the State colonization Society in Liberia, and collected specimens there and also in the Canary Islands. George Nash, head gardener at the New York Botanical Garden, collected in Florida and Haiti as well as in



(photo by A. B. Wellborn)

Closeup of *Hylocomium splendens*.

New York. Anna Murray Vail, librarian at the Garden, collected in New York before moving to France.

Perhaps the most interesting of the earlier collectors was Robert Statham Williams (Steere, 1945). At the age of 20, he moved out to the Montana wilderness where he was a homesteader, miner, explorer, and Pony Express rider. During the gold rush, he moved to the Yukon and became the first resident bryophyte collector. After trips to Peru, Bolivia, the Philippines and Panama, all in the early 1900's, he gave up his travels and worked for most of his remaining years at the New York Botanical Garden.

In the Adirondack region of New York State, much bryological exploration has taken place since Lesquereux's early mountain trips. Among the collectors near the turn of the century were Elizabeth Knight Britton, Charles H. Peck, Annie Morrill Smith, and Caroline Haynes. Elizabeth Britton, who was brought up in Cuba and later made many West Indian bryophyte collections, was largely responsible for building up the early bryophyte collections at Columbia University and the New York Botanical Garden. She did much collecting in the Adirondack high peaks area, particularly in the 1890's while staying in several of the early lodges, such as the Ausable Club Lodge, St. Hubert's, and Adirondack Lodge near Lake Placid. She collected in the heart of the mountains from these locations, as I have discovered by examining her herbarium specimens at the New York Botanical Garden.

Charles Peck, then State Botanist, published in 1898 an account of the plants of the town of North Elba, Essex County. This town includes several of the Adirondack high peaks, including Mt. Algonquin (McIntyre). He also commented on collections made on Whiteface Mountain, although this mountain is north of the town boundary. Peck listed 149 mosses and 32 liverworts, most of which were collected by Britton or himself. Other collectors included George Atkinson, mycologist and Cornell professor. Peck gave habitats as well as localities for the more unusual species. The localities given show that some of the best collecting areas for bryophytes, such as Mt. Algonquin and Indian Pass, were already well explored at this early date.



(photo by A. B. Wellborn)

Hylocomium splendens, a moss collected early in bryological exploration of the Adirondacks, by Peck on Mt. Marcy.

Annie Morrill Smith and Caroline Haynes also collected bryophytes in the Adirondacks in the early 1900's. Annie Morrill Smith studied botany in Europe, was editor of *The Bryologist* from 1900 to 1910, and eventually gave 20,000 moss and lichen specimens to the Brooklyn Institute of Arts and Sciences. In 1906, she published in *The Bryologist* a list of mosses from the vicinity of Little Moose Lake, near Old Forge in the western Adirondacks. In the same issue Caroline Haynes published a list of hepatics from the same region.

Much bryological exploration was also done in the Lake George region and the southern Adirondacks. One of the earliest collectors (1864-68) was Dr. E. C. Howe of Yonkers. Dr. Smith Ely Jelliffe collected in 1888-89 around Huletts Landing, and Dr. George Hulst, a Brooklyn botanist, at Assembly Point in 1898-99. Stewart Burnham (1919, 1920, 1929) of Hudson Falls published lists of bryophytes of the Lake George region. The region was broadly defined and

specimens from Washington, Saratoga, and even Essex and Warren Counties were included. Many bryologists were involved in the compilation of these lists, in addition to the above. Among them were George Clinton, Charles Peck, Elizabeth Britton, and also Wallace Greenalch of Albany, who collected in many parts of the State at the turn of the century. Burnham's own collections were first made in 1892 and were determined by Professor John Holzinger. Later, A. L. Andrews and Carl Warnstorf were involved in determining *Sphagnum* species; A. W. Evans and Caroline Haynes were among those determining hepatic species. Daisy Levy (1919) also published a separate list of mosses from Lake George.

It is clear that a great many bryologists were active in New York State and particularly in the Adirondack region prior to 1920. More recent Adirondack collectors include F. J. Herman, Stanley J. Smith, E. H. Ketchledge, Daniel Norris, Norton Miller, Richard Andrus, and myself.

All the early work on bryophytes in the State was floristic. That work continues and species new for the State and for the Adirondacks are still being discovered. In the checklist of the mosses of New York State compiled by E. H. Ketchledge (1957), the State was divided up into floristic districts based on latitude and longitude. A few more mosses have been discovered in the State since then, and there are many new district records, including a few from my studies. No similar published checklist is yet available for hepatics. Habitat information was given by some of the above authors, notably Peck and Burnham, but there is a lack of published ecological studies of bryophytes in New York State. In this respect, the present work is a pioneering venture; much of it could not have been carried out, however, without the floristic work of so many of these bryologists.

The Study of Species Diversity

Although diversity has long been of interest to biologists and naturalists, the interpretation of diversity has been a great challenge to ecologists in the past 15 years. Species diversity is of prime importance in understanding community structure and the dynamics of natural communities. Diversity, both in terms of species richness or variety (the number of species present) and of the relative abundance of these species, has been related to other important aspects of community structure. These include productivity, succession, stability, competition and habitat complexity. In addition to its theoretical importance in understanding community structure, diversity is also of practical importance for interpreting vegetation changes following human disturbance.

Species diversity has been studied in a great variety

of organisms including diatoms, insects, fish, lizards, birds, mammals, and vascular plants. Vascular plant studies relevant here include those by Johnson, Mason, and Raven, 1968; Whittaker, 1965, 1969; Pielou, 1966, 1969; Monk, 1967; Monk, Child, and Nicholson, 1969; Johnson and Raven, 1970; Auclair and Goff, 1971; Risser and Rice, 1971; Reiners, 1972; Shafti and Yarranton, 1973; Nicholson and Monk, 1974; and Siccamo, 1974. Most of the vascular plant work deals largely with tree diversity, although several of the above also include shrubs and herbaceous vascular plants.

Few diversity studies have been carried out on non-vascular plants other than phytoplankton. Nash (1972) discussed lichen species diversity in relation to pollution; Hoffman (1971) discussed diversity of epiphytes on Douglas fir, and a study of plant diversity in Alaska by Reiners, et al., includes bryophytes. Nonvascular plants, and especially bryophytes, show high species richness in many different habitats, and constitute a relatively important component of the vegetation at a variety of latitudes, as, for example, in tropical and temperate rainforests, boreal bogs, and Arctic tundra. The relationships of bryophytes to other primary producers in a community have been explored to some extent in terms of biomass (Bliss, 1966) but not in terms of diversity or of theoretical aspects of community structure.

Phytosociological studies of bryophytes, or analyses of vegetation in which bryophytes are recognized as an important component, have been carried out especially in Europe (Dahl, 1957; Gimingham, 1966; Yarranton, 1967a) and in Canada (Stringer and LaRoi, 1970; Yarranton, 1970; Neal and Kershaw, 1973; Stringer and Stringer, 1973).

Bryophytes differ from most vascular plants in some aspects of their basic biology: nutrient procurement (lack of roots), dispersal (spores, swimming sperm, vegetative propagules) and genetic system (dominance of haploid plant). It seems likely that some of these differences cause bryophytes to play a different role in community structure from vascular plants of similar size. The present study was undertaken to elucidate diversity relationships among bryophytes, and the relation of bryophytes to the structure and evolution of communities in which they are found.

Some basic questions can be asked about diversity in the Adirondack and Helderberg plant communities analyzed in the present study. Trees, shrubs, and herbaceous vascular plants as well as bryophytes were included. For example, by sampling a particular segment of a community, e.g., vascular plants, is one "obtaining an index to the overall diversity of the system" (Johnson and Raven, 1970)? Are diversity patterns for shrubs, for example, similar to those for bryophytes as

one ascends Whiteface Mountain? Is species number a sufficient indicator of diversity, or is an evenness component, based on the relative abundance of the species present, also important? This evenness component of diversity has also been related to the question of whether certain groups of organisms consist largely of opportunistic or equilibrium species (Tramer, 1969). The present study provides data on this question for bryophytes, some of which are considered opportunistic on other grounds (Schofield, 1971; Schuster, 1966).

Other questions concern taxonomic diversity. Should all species be considered ecological equivalents in terms of diversity? Should a forest with three species of oaks as dominants or a bryophyte community with three species of *Polytrichum* be considered as diverse as one with three dominants, each belonging to a different genus?

If there are relatively few species in a community, as, for example, in the arctic-alpine communities above timberline, are the species more likely to belong to different genera than if there are many species? Such questions of taxonomic diversity have been explored for other organisms (Lloyd, Inger, and King, 1968; Simberloff, 1970) but not previously for bryophytes.

In many previous studies, attempts have been made to correlate diversity with environmental factors, both biotic and abiotic. This has not been done for bryophytes except in specialized communities, such as bryophytes of bogs (Vitt and Slack, 1975) or epiphytic bryophytes (Hoffman, 1971). I have studied bryophyte diversity in relation to a number of such factors in the Helderbergs (Kenrose Preserve), part of the present research.

Several workers have attempted to determine the variables affecting species diversity in a particular region using multiple regression analyses. Such studies largely concern birds or vascular plants. I have made a similar analysis of mosses of New York State, using the checklist compiled by Ketchledge (1957), based on districts into which the State has been divided for floristic studies. Variables used in the analysis and results obtained are discussed below. One result, that the range of elevations within a district is an important determinant of diversity, was used in setting up my field studies. These studies included gradient analysis of bryophyte diversity in relation to other environmental factors. Biotic factors such as diversity of other primary producers in the community have also been considered. The methods used in these studies are described in the following sections.

The Study Areas

Adirondack Areas—Whiteface and Ampersand Mountains

Adirondack field studies were carried out in the two floristic districts with the greatest range of elevation in New York State, districts 3 and 4 (see map, fig. 1). These districts include the Adirondack high peak area, including the highest mountain in the State, Mt. Marcy, 5344 ft (1629 m). The summits of this mountain and of several other Adirondack peaks including Whiteface Mountain, 4867 ft (1484 m) are above timberline and support an arctic-alpine flora. One major part of this study was conducted on Whiteface over an elevation range of 1600 to 4800 ft (488–1463 m). Whiteface, the fifth highest peak, is located at 44°21', ten miles north of the major high peak area of the Adirondacks. As a solitary peak it is more exposed than the other mountains in that area, and the summit is particularly subject to rigorous climatic conditions.

The winter is long and the growing season correspondingly short, only 80–105 day in this part of the Adirondacks (Stout, 1956; Feuer and Hager, 1956; Hartwig and Peech, 1963). At the higher elevations of Whiteface, it may average only 50–70 days (Nicholson and Scott, 1969). I have seen several feet of snow in June in the balsam fir (*Abies balsamea*)¹ forest at 4400 ft (1341 m) on Whiteface.

The other Adirondack study area was Ampersand Mountain in district 3, south of Saranac Lake (see map, fig. 1). This mountain, just over 3300 ft (about 1000 m) shows little sign of disturbance by fire, logging, or other human activity. Epiphytic vegetation is well developed on this mountain, bryophytic epiphytes occurring on a variety of hardwood and conifer trees. These epiphytes were also included in the present study. The elevations studied on Whiteface and Ampersand Mountains overlap between 1600 and 2800 ft (488–854 m) so that both hardwood forest and spruce-fir forest vegetation could be compared on the two mountains.

Heimberger described the vegetation types for the Adirondacks (1934), but little work was published on the Adirondack forest for the next 30 years. Since 1963, a large scale study of the vegetation of the Whiteface area, particularly in relation to topographic gradients has been conducted (France and Lemon, 1963; Holway, Scott, and Nicholson, 1964; Scott and Nicholson, 1969; Scott and Holway, 1969; Nicholson and Scott, 1969; Breisch, et al., 1969). Soil (Witty,

¹ Names of vascular plants follow Fernald, M. L. 1950, Gray's Manual of Botany, American Book Co., New York, with the exception of *Quercus borealis* Michx.f. and *Betula alleghaniensis* Britt.

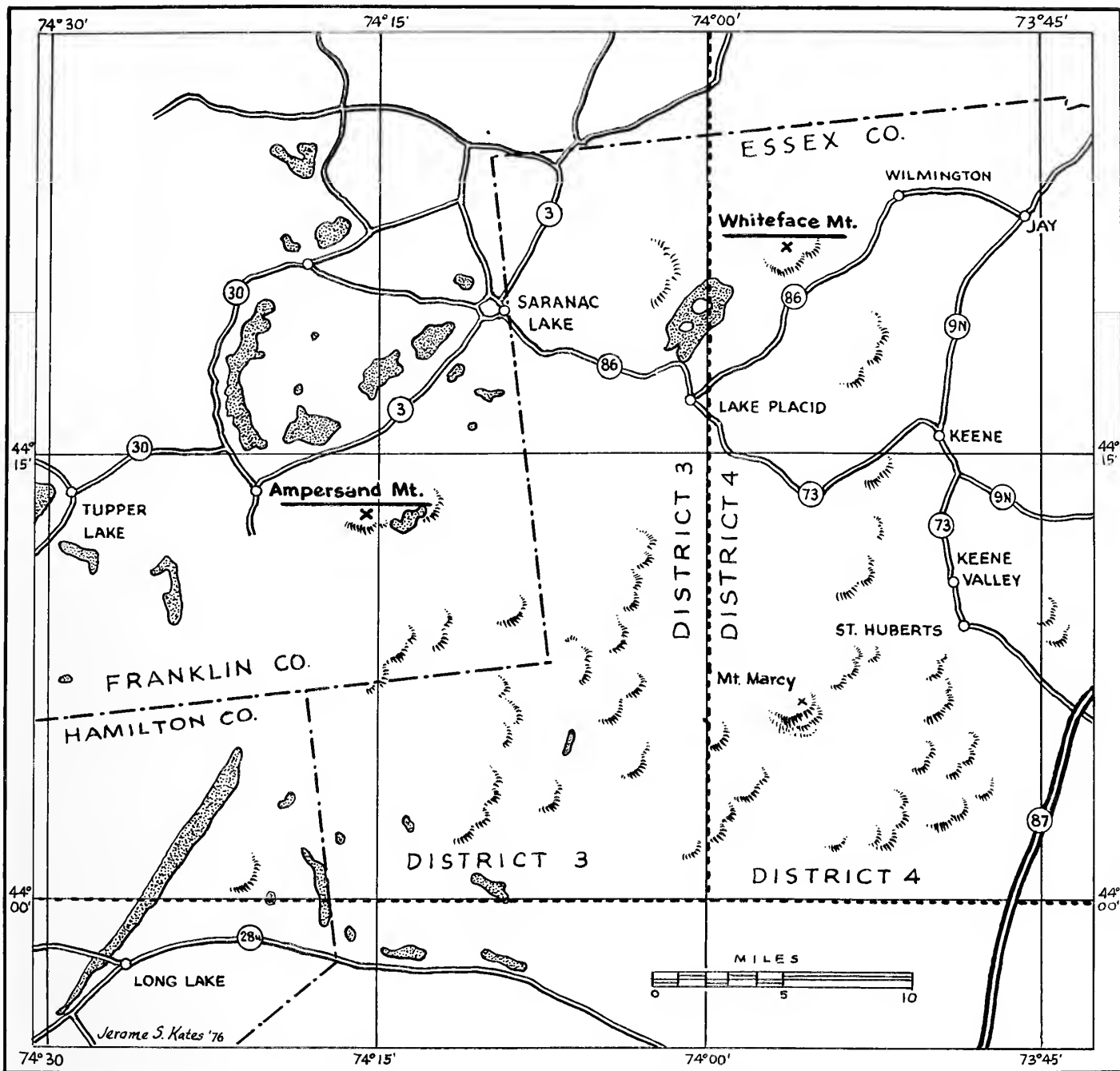


FIGURE 1 Whiteface Mt. and Ampersand Mt., sites of Adirondack field studies. By Jerome S. Kates.



(photo by N. G. Slack)

Deciduous forest of considerable *Betula papyrifera*, along Wilmington trail, Whiteface Mountain.

1968) and weather data (Falconer, 1963) have also been published. Very little of the published work bears directly on diversity of bryophytes. According to the above authors, nonvascular plants were not included in their studies because of the difficulty of identification.

The Wilmington trail area of Whiteface Mountain, in this study, has not been damaged by tourists; it is, in fact, much less used than the trails in the Marcy-Algonquin region of the Adirondack high peaks. Summit disturbance is confined to the relatively small area visited by tourists; no quadrats were established in that area. The great majority of the area above timberline is undisturbed except by natural rockslides. Some areas at lower elevations on Whiteface, particularly between 2000 and 2500 ft (about 600–750 m) are undergoing secondary succession, probably as a result of fire, as indicated by the presence of *Betula papyrifera*, *Populus grandidentata*, and other successional trees. Disturbance is not recent; there have been no major fires here for at least 50 and probably 70 years (Holway, Scott, and Nicholson, 1969). There has been no lumbering since 1896 when protective forest legislation was established. By using one of these areas, bryophyte diversity and species composition could be compared for “disturbed” and “undisturbed” areas (or earlier and later stages of succession of canopy trees) at the same elevation. I have made this comparison both on Whiteface and between Whiteface and Ampersand Mountains.



Base of Whiteface Mountain trail, near Wilmington, N.Y.; hemlock-hardwood forest.

Helderberg Area: Kenrose Preserve

The third area I used in this study was Kenrose Preserve, a deciduous forest area on the Helderberg plateau. It is the property of The Nature Conservancy and is located in the Rensselaerville Quadrangle (U.S.G.S.) in West Berne, New York, west of Albany (42° 36'N, 74° 12'W). Although the whole preserve is on Hamilton shale and is completely within the Deciduous Forest Formation (including Hemlock-hardwoods, Braun, 1950), there is much variation in tree composition. Forest types include oak-hickory, beech-maple, hemlock, and other combinations of dominants. The elevation range is from 1120–1500 ft (335–457 m).

The vascular flora of Kenrose Preserve was studied quite extensively in 1968–69 by Carl George, Robert Carlson and their students (unpublished manuscript). They set up permanent quadrats for the purpose of establishing a base line for future vegetation studies. Some of their vascular plant and environmental data are used in conjunction with my bryophyte data in the present study.

Field Methods

Adirondacks

Quadrats were set up on both Whiteface and Ampersand Mountains at 400 foot (122 m) elevation intervals beginning at 1600 ft (488 m), with two quadrats at each elevation. In addition, five quadrats were set up in the arctic-alpine summit area on Whiteface. The quadrat size was five by eight meters. I selected this large quadrat size because it was adequate for sampling vascular ground flora as well as bryophytes, and also because bryophytes were rather sparsely distributed at some elevations. With the large quadrats, I was able to compare bryophyte cover at different elevations and in different forest types.

As it was not possible to place transects straight up the mountains, quadrats were placed perpendicular to and at a predetermined distance from the trail, where the trail reached the selected elevations. At these distances, eight meters on Whiteface and 15 meters on Ampersand, there were no apparent disturbance effects of the trails. Because quadrats were regularly placed, there was no possibility of choosing them either for bryophytes or forest type, except as these are influenced by elevation, the independent variable in the study. Quadrats were delineated with iron spikes and copper wire and are relocatable.

Quantitative methods were used to record bryophytes as well as vascular plants. Vascular plants were counted as individuals in all quadrats except those on

the summit of Whiteface (see below). For some plants, e.g., *Ribes glandulosa*, it was difficult to determine what constituted an individual. In such cases, separate stems were counted. It is rarely possible to accurately determine what constitutes an individual bryophyte plant; therefore, cover was measured for bryophytes. The area covered by each species was computed by measuring length and width, radius, or triangle base and height for variously shaped clumps. I have found these methods repeatable to within five percent accuracy. Actual measurements are more precise than estimates using a cover scale, especially since cover scale data are often converted into percentage cover by statistically questionable techniques. In addition, many bryophyte species, e.g., *Ptilidium pulcherrimum* or *Dicranum montanum*,¹ are present in numerous small pieces within a quadrat, so that cover is hard to estimate. In the summit areas of arctic-alpine flora, cover measurements were used for vascular plants as well as for bryophytes because all the plants occurring there, e.g., *Vaccinium uliginosum*, have a clumped or caespitose growth form and cannot be counted as individuals.

Studies made at only one season may underestimate total diversity. Whittaker (1965) found this to be especially true for winter ephemerals in the desert. In order to find out whether spring ephemerals were significant in the Adirondacks, I restudied several quadrats on both mountains. Spring data were compared with those of the previous summer and fall to determine the extent of seasonal diversity.

Certain specialized bryophyte habitats are not represented or are underrepresented in a large study of this type. One such habitat is that for epiphytic bryophytes, living trees. I have collected data on species richness of epiphytic bryophytes on Ampersand Mountain. The epiphyte study is discussed separately below.

Helderbergs

At Kenrose Preserve, George and Carlson had set up permanent stations and quadrats. I relocated and used 13 of their original stations, all in wooded areas. George and Carlson (unpublished data) recorded the number of individuals for each species of vascular plant, using five 12 by 48 foot quadrats at each station. They also collected soil and micro-climatic data for each station. These collected soil type, pH, and nutrient content; soil and air temperature; relative humidity, and light intensity. (For further details of the design of this original study see Slack, 1971.) In the present study, I have used 4 by 16 meter quadrats, but

¹ Names of mosses follow Crum, Steere, and Anderson, 1973, and of hepatics, Schuster, 1953.

Analysis of Data

Diversity Indices

The term “species diversity” has been used for two different types of measurements. The first type, which measures species richness, is sometimes called a variety index (Auclair and Goff, 1971). It is essentially based on the number of species per area. (Gleason, 1922; Willis, 1922; Margalef, 1957; Menhinick, 1964) or on species number and a hypothetical distribution of relative abundance (Fisher, Corbet and Williams, 1943; Preston, 1948, 1962). Number of species (signified by S) is used in the present study.

The second type of index includes an evenness or equitability component in that the relative abundances of the species in the sample are included in these measures. The most commonly used of these came originally from information theory. Margalef (1957) suggested an analogy between diversity in biological communities and “information” content. The usefulness of this analogy and the biological meaning of diversity, particularly in regard to stability, has been questioned (Paine, 1969; Pielou, 1969; Auclair and Goff, 1971; Hurlbert, 1971; Goodman, 1975). The indices themselves, however, have been used in studies with many kinds of organisms as empirical measures of species richness and relative abundance of species. When used in this way the information theory type of measure is considered a “more meaningful index when used as a comparative statistic within taxonomically restricted groups” (Goodman, 1975). The index most often employed by ecologists and therefore most useful as a comparative statistic is Shannon’s formula (Shannon and Weaver, 1963):

$$H' = - \sum p_i \ln p_i \quad (1)$$

where p_i is the proportion represented by the i^{th} species. This is the diversity index I have used in the present research. Pielou (1966a, 1966b, 1969) has discussed the use and misuse of this and similar indices for different types of biological collections. The use of this form of Shannon’s index is justified in terms of the sampling methods used in this study. Several workers have compared this index and other diversity indices such as Simpson’s (1949) and McIntosh’s (1967) using the same data and found very high correlations among them (Auclair and Goff, 1971; Nicholson and Monk, 1971; Gauch, Chase, and Whittaker, 1974). It appears that in spite of somewhat different theories on the part of their authors, these indices measure essentially the same parameters.

Measures of Importance

In Shannon’s formula (1, above) the term p_i refers to the proportion of the total number of individuals (or



(photo by C. J. George)

Kenrose Preserve, showing one of the slopes studied.

have collected data for the included 12 by 48 foot quadrats as well. The small extension made virtually no difference in the diversity index results; bryophytes are relatively sparsely distributed in the whole area as compared to the Adirondack sites.

At least one 4 by 16 meter quadrat was sampled for each station. At six of the 13 stations, at least two quadrats were sampled in order to compare within-station and between-station variation in diversity and species composition. Twenty quadrats were completely sampled for bryophytes, using the same cover measurements as explained above for the Adirondack quadrats. The study was set up to include pairs of stations at the same elevations so that I could determine whether elevation differences over the relatively small range of 1120 to 1510 ft (335–457 m) are statistically important determinants of diversity.

total biomass, cover, etc.) belonging to the i^{th} species. The number of individuals has usually been used, particularly in the study of bird diversity (e.g., MacArthur and MacArthur, 1961; MacArthur, 1964; Tramer, 1969; Recher, 1969), by other animal and plankton ecologists (e.g., Lloyd, Inger, and King, 1968; Margalef, 1968), and in most plant studies (e.g., Pielou, 1966a; Nicholson and Monk, 1974). I have used proportions of individuals for vascular plants in the present study except in the alpine quadrats. For alpine vascular plants and for bryophytes, I have used proportion of cover for each species.

Other measures of relative importance have been suggested for both animals and plants, particularly where there are large differences in size among the species sampled (Dickman, 1968). I have treated trees, shrubs, and herbaceous plants separately in most analyses, eliminating the relative size problems. Cover measurements do underestimate the importance of tall clump-forming species as compared to prostrate pleurocarpous mosses with the same cover value. It would be possible to measure height as well as area covered and compute a volume for use in the index. Alternately, one could harvest the bryophytes and use biomass (dry weight) or energy (caloric value as measured in a calorimeter). Forman (1968) has attempted to correlate cover measurements with biomass and caloric value on a species basis, but results are not entirely consistent; Bliss (1962) and Forman (1968) found somewhat different values for *Polytrichum juniperinum*, the only species used in both studies. Variations in growing conditions probably affect the cover-biomass-calorie relationships.

Biomass has been used as a measure of importance in tree diversity studies (Wilhm, 1968). Since a very high percentage of tree biomass consists of dead xylem tissue, the values are out of proportion to the present dynamics of the community. Whittaker (1965, 1970) has championed the use of productivity measurements and has used these successfully for both woody and herbaceous plants (Whittaker, 1965, 1966; Whittaker and Woodwell, 1969). From a theoretical point of view, productivity (or net photosynthesis for primary producers) per unit time is probably the best measure of the importance of a species in a community. It is, however, difficult to obtain the necessary data for a large number of different species. Tree productivity is usually estimated by using dimension analysis as Whittaker and Woodwell (1969) have done.

Productivity measurements are especially difficult to obtain for bryophytes because information on growth rates in the field is available for only a few species (Longton and Greene, 1969). Furthermore, in contrast to the situation in most vascular plants, it is often extremely difficult to ascertain what constitutes the current year's growth. Techniques worked out by Watson

(1975) for *Polytrichum* species might be useful here. Without biochemical tests involving the breakdown of chlorophylls to pheophytin, it is often impossible to tell what portion of a moss is alive, and even such tests are not discriminating in certain genera such as *Sphagnum*. Although progress is currently being made on productivity measurements for bryophytes in the Arctic, it is doubtful that these measurements will ever be feasible for as many different species as were encountered in the present study. For the present, cover measurements appear to be the best available for bryophytes for use in diversity studies. However, volume measurements may be preferable when there are striking differences in height among species. Biomass measurements of living material are perhaps equally suitable, but these require destruction of the community, or a portion of it, in the process of studying it. Such measurements have recently been used successfully for studies of epiphytes on old-growth *Pseudotsuga* (Denison, et al., 1972; Pike et al., 1975).

The Evenness Component of Diversity

Lloyd and Ghelardi (1964) and others (Kricher, 1972; Murdock, et al., 1972) have pointed out that it is desirable for some purposes to be able to isolate the relative abundance component of diversity as measured by Shannon's index. Margalef, under the subject of "redundancy," had already pointed out the importance of this component in his original 1957 paper. The ecological meaning of this evenness (or equitability) component has been the subject of considerable discussion (Sager and Hasler, 1969; Tramer, 1969; Hill, 1973). Some of this discussion concerns the relationship between the evenness component of diversity and opportunistic versus equilibrium species groups. This question will be explored further in conjunction with my results for bryophytes.

The measure for evenness used in the present research is

$$J' = H'/H' \max \quad (2)$$

where $H' \max = \log_e S$. Pielou (1966a) suggested using $H'/H' \max$ to measure evenness of distribution of species abundance, and Tramer (1969) subsequently called it J' . J' is not based on any hypothetical ecological maximum for evenness, and has the further advantage of being the most widely used measure; therefore, comparisons can be made with other research.

(Note: $H' \max$ represents the maximum possible diversity for a given number of species (S); i.e., the value of H' if all species were equally abundant. For further discussion of this and other evenness or equitability measures see Slack, 1971.)

Comparison of Species Composition

Diversity indices themselves cannot tell us anything about changes in the actual species composition. We may find, using Shannon's formula, that the diversity of bryophytes is almost the same for quadrats at 1600 ft (490 m) and at 4000 ft (1220 m) on Whiteface Mountain, but this gives no information about floristic similarity at the two elevations. Southwood (1964) reviewed a number of indices for comparing faunas (or floras) over space or time. Two types of indices have been used. One group, collectively called Coefficients of Community, are based solely on species presence. These include those of Jaccard (1922), Kulezynski (1928) and Sørensen (1948). The latter, a variant of Jaccard's, as pointed out by Dahl (1960), has been most often used:

$$\text{Sørensen's Quotient of Similarity (Q.S.)} = \frac{2w}{m + n} \quad (3)$$

in which m is the total number of species in the first sample (or quadrat), n the total number in the second, and w the number of species common to both samples

The second type of index uses the relative abundance of the species in the sample, not merely their presence, in making comparisons. In so doing it tends to emphasize the importance of dominant species in weighting similarity between samples. An often used measure of this type is the Percentage of Similarity (Raabe, 1952)

$$\text{Percentage of Similarity} \\ (\% \text{ Sim.}) = \sum \min(a, b, \dots x) \quad (4)$$

where \min = the lesser of the two percentage compositions for species $a, b, \dots x$ in the two samples. For example, given the following percentage compositions or two quadrats A and B having species a, b , and c :

	a	b	c		a	b	c
case 1 A	.95	0	.5	case 2 A	.95	0	.5
B	.20	.75	.5	B	.75	.20	.5

the % Sim for case 1 = .20 + 0 + .5 = .25

whereas Sørensen's Q.S. = $2(2/5) = .80$

the % Sim for case 2 = .75 + 0 + .5 = .80

whereas Sørensen's Q.S. remains the same

Thus it can be seen that the Percentage of Similarity index (4) rates as most similar those samples (quadrats) that have similar dominants. In this example, Sørensen's index (3) appears to overvalue the rare species

(species c in both cases 1 and 2 above) as pointed out by Whittaker and Fairbanks (1958). This is not always so, however. A large number of rare species can give low Sørensen values as compared with Percentage of Similarity for the same quadrats. Comparison of the two types of indices have been made by Kontkanen (1950) for leafhoppers and by Whittaker and Fairbanks (1958) for freshwater plankton. Kontkanen found the Coefficient of Community type of index more satisfactory; Whittaker and Fairbanks, the Percentage of Similarity. The group of organisms with which one is working is probably the important factor.

I have used both Sørensen's index and Percentage of Similarity as well as two variants of Sørensen's with my data. These variants involve the calculation of Sørensen's index using only those species which, respectively, constitute at least 1 percent (referred to as Sør. .01) and at least 5 percent (Sør. .05). The objective was to compare the effectiveness of all four methods in evaluating floristic similarity. The latter two methods evaluate the effect of the inclusion of rare species. Cluster analysis was used to compare these measures of floristic similarity. The method used was essentially a modification of Harmon's B-coefficient (Fruchter, 1954; Slack, 1971).

In addition to the above methods, which all compare quadrats in pairs, I have used a method of Dahl's (1960) to compare the vegetation, both bryophyte and vascular, of Whiteface Mountain with that of Amper-sand Mountain, and the vegetation of both Adirondack sites with that of the Kenrose Preserve. The deciduous forest, spruce-fir forest, and arctic-alpine vegetation were compared both within and among the areas (Slack, 1971).

Taxonomic Diversity

A question was raised in the introduction as to whether all species are ecological equivalents in terms of diversity; e.g., is a bryophyte community with three species of *Polytrichum* (or *Sphagnum*, or *Dicranum*) as dominants as diverse as one having three dominants each belonging to a different genus? One way in which this question can be examined is in terms of niche separation; congeneric species with widely separated niches can, it seems to me, be considered ecological equivalents of species in different genera in terms of diversity. Congeneric bryophytes in genera such as *Dicranum*, *Polytrichum*, *Grimmia*, and *Brachythecium* were found in the same quadrats in this study. I have examined these genera in regard to possible niche separation.

Quantitative analyses of taxonomic diversity can also be made. I have calculated the number of congeneric species in a quadrat in relation to the total number of species in that quadrat. In bird studies (Grant, 1969), the proportion of congeners has been found to vary di-

rectly with the total number of species; it was not known whether this was true for bryophytes.

In addition, total species diversity (H') for bryophytes in each quadrat has been partitioned into specific, generic, and familial portions, as was done by Lloyd, Inger, and King (1968) for frogs, lizards, and snakes in the Borneo rain forest. These calculations are subject, of course, to decisions of taxonomists as to what constitutes a genus or a family. Family lines in particular are in considerable dispute for bryophytes, and some larger genera have been especially subject to splitting, for example, *Lophozia*, *sensu latu*. Species lines are in general less of a problem with most genera of bryophytes. Hybridization appears to be uncommon in bryophytes (Khanna, 1962; Williams, 1966).

Gradient Analysis

The major gradient used in this study was elevation. Changes in bryophyte and vascular plant vegetation were analyzed in relation to elevation. These changes included the following: changes in species richness (S) and in species diversity (H'); changes in species composition; changes in relative cover of bryophyte species. Comparisons of species composition at different elevations were made by using Sørensen's and Percentage Similarity indices as explained above. Other methods were graphical and are self-explanatory.

Multiple Regression Analysis

Multiple regression analyses were carried out in regard to determinants of species richness in bryophytes both for New York State as a whole (see following section) and for Kenrose Preserve. In Kenrose Preserve, a large number of abiotic and biotic factors were used in the regressions. A stepwise multiple regression program (STEPREGI: SUNYA code: STAT/02) was used. Correlation coefficients between bryophyte diversity (H') and environmental and other parameters were also calculated.

Bryophyte Diversity in New York State

Bryophyte diversity in the whole was examined by means of a multiple regression analysis of data from Ketchledge's (1957) checklist of mosses of New York State. Since there are no comparable data for hepatics, this analysis is restricted to mosses. The checklist gives the moss species present in each of the districts of New York State (see fig. 2) as determined from herbarium and field studies. These data are largely free of taxonomic problems; the specific status of only a few

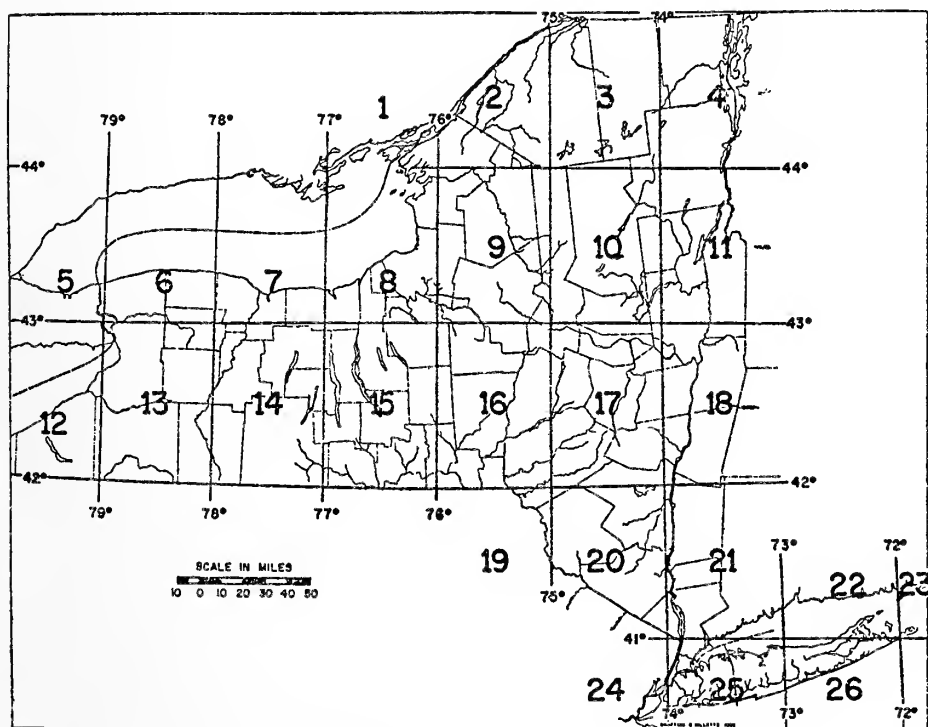


FIGURE 2 Floristic districts of New York State, from Ketchledge, 1957.

taxa is in doubt. Some of the districts, however, had been better explored than others, for example, those close to New York City and to Cornell University. Moreover, additional species have since been discovered for various districts, including a few that I found in the three districts involved in my studies. Nevertheless, these are probably the best data of this sort available for American bryophytes.

The parameters used in the linear regression analysis of these data were latitude, area, and the range of elevations within one district. The range of elevations ("elevation range" on the table) was obtained from topographic maps (USGS) of the State. Areas of districts were determined by planimeter measurements from State roadmaps.

Results of the multiple regression analysis are shown in table 1. In this table r^2 and R^2 are the coefficients of determination and multiple determination, respectively. It can be seen that range of elevation acts as a major determinant ($r^2 = 0.5159$) of moss diversity in terms of species richness (S). Area adds very little as a determinant ($R^2 = 0.5665$).

TABLE 1

Coefficients of Determination (r^2) and
Coefficients of Multiple Determination
(R^2) from Multiple Regression Analysis
based on Checklist of the
Mosses of New York State

Parameters	r^2	R^2
Area	0.3745	
*Latitude	0.0001	
Area with Latitude		0.3748
Elevation Range	0.5159	
Elevation Range with Area		0.5665
Elevation Range with Area and Latitude		0.5679

*Latitude is not a significant variable.

Although there is a latitude range of almost five degrees in New York State, latitude is of no importance as a predictor of diversity ($r^2 = 0.0001$). A few species may be affected by latitude. *Pogonatum brachyphyllum*, a coastal plain species is found only as far north as Long Island, and there are old records for such southern species as *Syrrophodon floridanus* and *S. texanus* in the southernmost districts (Ketchledge,

1957). Two far northern species, *Aulacomnium turgidum* and *Conostomum tetragonum* are found in a northern district, but at elevations over 5000 ft (1525 m). Their presence is almost certainly an effect of elevation, not latitude; no unusual species are found in the northwestern districts of the State, which are at the same latitude but do not include the higher elevations.

Area has surprisingly little value as a predictor of species richness, in contrast to the results of other studies, particularly island studies, in which area was the most important predictor. These include bird studies (Hamilton, Barth, and Rubinoff, 1964) and vascular plant studies (Johnson, Mason, and Raven, 1968; Slack and Nicholson, in preparation). Hamilton, et al., (1963) did find elevation more important than area for vascular plants of the Galápagos, but this conclusion has been questioned (Johnson and Raven, 1973) because of the inadequacy of the plant data used. Vuilleumier (1970) studied bird species richness on continental "islands," páramo vegetation on isolated mountain tops. He, too, found area, together with distance from the source, the important predictors of species richness.

Since this is not an island study, distance from the source of the vegetation is probably not a factor in New York State. It probably is a factor, however, in comparing species richness of bryophytes in New York and in the Southern Appalachians, or for example, in the Adirondacks and the Southern Blue Ridge (Slack, 1976). Larger area provides a larger target size for propagules and also more spacial heterogeneity, resulting in a wider range of habitats. The problems of immigration and establishment, so important for island species, are less important for bryophytes in New York State as a whole, except for species restricted to special "islands." Principles of island biogeography do apply to *Sphagnum* and hepatic species restricted to bogs and to those bryophytes found in tundra areas above timberline on Adirondack high peaks. (From my own experience this seems to be true. More arctic-alpine species of both vascular plants and bryophytes are found on the extensive tundra areas of Marcy and Algonquin than on peaks with less extensive areas. More *Sphagnum* species are found in the extensive Bloomingdale Bog area than in smaller bogs. Specific data are needed, however.) Apart from these special circumstances, it can be seen that area alone is not the important determinant by examining adjacent districts of essentially equal area—districts 14, 15, 16, and 17 (see fig. 2). Species richness varied in these districts from 102 to 281 species. Three of the smaller districts (4, 11, and 18), on the other hand, are among the five having the highest number of species in the State.

As shown in table 1, range of elevation was the best determinant of moss diversity. Those districts with the greatest elevation range, districts 3, 4, and 17 in the Adirondack and Catskill Mountains, all had high numbers of species—180, 266, and 281, respectively. Two of these districts were used in the present study in order to investigate further and more specifically the effect of elevation in relation to both moss and liverwort diversity. Another indication of this relationship within an area comes from a survey of the literature on latitudinal diversity of bryophytes (Slack, 1971). The number of bryophyte species reported for 31 different geographical regions at all latitudes was given together with the area of each region. Although the data for many of these areas, especially tropical ones, are admittedly incomplete, a number of tentative conclusions could be drawn. The one relevant here was that species richness is greater in regions of greater elevation range and low evapo-transpiration rates. Two more recent publications, giving compilations of the mosses of Japan (Iwatsuki and Noguchi, 1973) and of the Southern Blue Ridge of southeastern United States (Anderson and Zander, 1973) further substantiate these conclusions.

The regression analysis leaves a large part of the variance in species richness unexplained. It seems likely that a variable indicating the amount of bryological exploration for each district up to 1957 would have been helpful. When a new checklist is published with data collected since 1957, this analysis should be rerun. In addition, climatic factors such as annual precipitation (or precipitation in relation to temperature) could be added to the analysis. Variables indicative of spatial heterogeneity, such as types of rock outcropping, might also be important.

That elevation range is an important determinant of hepatic as well as moss diversity has been brought out in the field studies I conducted in New York State. The results of these studies will now be presented.

Results of the Adirondack Studies

Summary of Results

The results of the field studies, outlined here, are discussed in more detail under the separate headings below. A greater diversity of bryophytes occurred in a larger range of elevations. Increased overall diversity largely resulted from changes in species composition of bryophytes with change in elevation and, therefore, with forest type. Throughout the elevation range, species composition changed with increasing elevation difference between the quadrats sampled. Although a

few species occur throughout the elevation range, I identified several distinct distribution patterns for bryophyte species by plotting their relative abundance at different elevations. Both species present and abundance varied with elevation. Species composition of bryophytes in deciduous forest was similar both between quadrats on one mountain and between mountains; this was true, but to a lesser extent, for coniferous forest. Arctic-alpine quadrats showed considerable variation in species composition, and almost no similarity existed between arctic-alpine and coniferous forest bryophyte communities.

Diversity, whether measured by S or H' (see page 8), showed different patterns along the elevation gradient for each of the plant groups studied: bryophytes, trees, shrubs, tree seedlings, and herbaceous vascular plants. S and H' also showed somewhat different patterns for any one group. For bryophytes, H' changed very little up to 3600 ft (1100 m). High elevation balsam fir quadrats with late snow cover showed highest diversity (both S and H') largely because of an increase in the number of species of hepatics. Both mean and maximum number of moss species per quadrat were similar for deciduous and spruce-fir forest, but lower in the arctic-alpine quadrats. For hepatics, species richness was higher in the coniferous than in deciduous forest, and lowest in the arctic-alpine summit quadrats although some species are restricted to this elevation.

In the deciduous forest at 1600 ft (490 m), S and H' were about equal for bryophytes and for all vascular plants together; at all other elevations, bryophyte diversity was higher than that of vascular plants.

The evenness component of diversity (J') varied greatly; in some circumstances extreme dominance by one species resulted in very low J' and lower H' values. Most of the J' values were lower than reported by other investigators for birds and for vascular plants.

Diversity was not correlated with bryophyte cover (a long-term measure of productivity) for the whole elevation range. There is some indication, however, substantiated by the Kenrose results (see page 40), that within a deciduous forest area, H' is positively correlated with total percent of bryophyte cover.

An inverse relationship was found between shrub and tree diversity and that of bryophytes, indicating interaction between these groups of plants. Competitive interaction between a bryophyte, *Pleurozium schreberi* and an herbaceous plant species, *Oxalis montana* was also studied.

Seasonal diversity, the epiphyte study made on Ampersand Mountain, and taxonomic diversity are each discussed separately below.

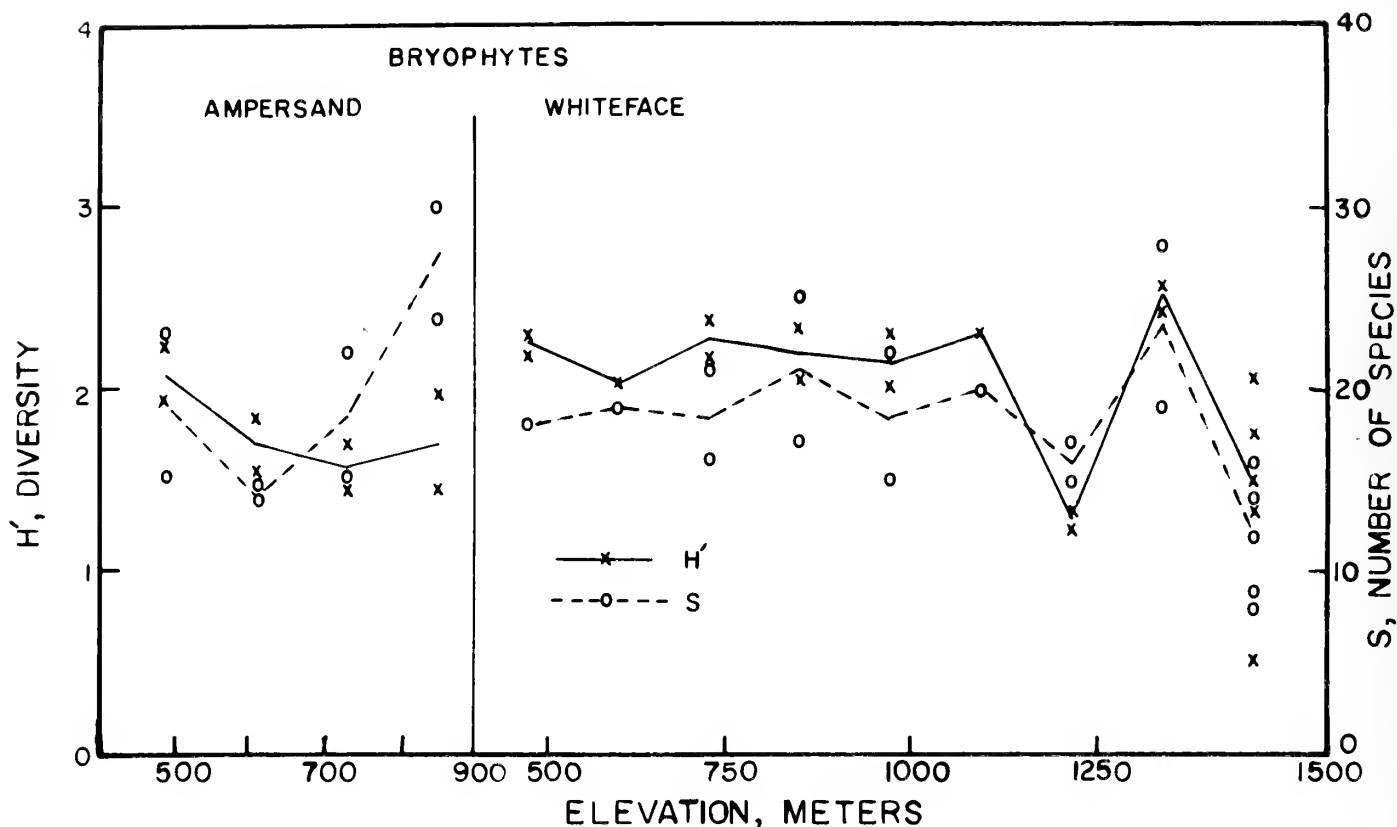


FIGURE 3 Changes in species richness (S) and diversity (H') with elevation for bryophytes at Whiteface and Ampersand Mts.

Elevation in Relation to Diversity

Figure 3 shows changes in species diversity in terms of species richness (S) and for the Shannon function (H'). The latter contains an evenness component as explained above. Data for Ampersand and Whiteface Mountains are shown separately. H' is seen to change surprisingly little from 1600 ft (490 m) to at least 3600 ft (1100 m) on Whiteface. At 4000 ft (1220 m) there was a sharp drop in H' with, however, little change in the number of species, S. The low diversity (H') is due here to the high dominance of one species, *Pleurozium schreberi*, which accounts for 59 to 67 percent of the total bryophyte cover. The resulting evenness values are very low, $J' = 0.44$ to 0.49 .

At 4400 ft (1340 m) on the other hand, both H' and S increase. At that elevation, where there is dense *Abies balsamea* forest and very late snow cover until mid-June or later, an unusually high number of hepatic species increase the diversity.

I studied additional quadrats at these elevations after the completion of the main study to determine whether the findings at these two elevations might be chance effects of sampling. Very similar results were obtained in this resampling at the same elevations:

4000 ft (1220 m): first sampling $H' = 1.33$
second sampling $H' = 1.25$

4400 ft (1340 m): first sampling $H' = 2.63$
second sampling $H' = 2.41$

The latter value (2.41), though not as high as in the first quadrat at 4400 ft, is nevertheless higher than that for any other elevation in the whole study.

The arctic-alpine quadrats vary greatly in diversity (H'). Many factors such as microtopography, slope aspect, wind exposure, snow and water retention changed over very short distances on the summit of Whiteface, producing a mosaic of vegetation. These factors are important in determining the vegetation types, both on Whiteface (Nicholson, 1969) and in the alpine communities of the White Mountains (Bliss, 1963). In general, both H' and S are lower than in the deciduous forest or the spruce-fir, or in pure fir at 4400 ft (1340 m), but considerable variation was found



(photo by A. B. Wellborn)

Author working in krummholz zone, Whiteface Mountain. *Andreaea rupestris* on rock in foreground.



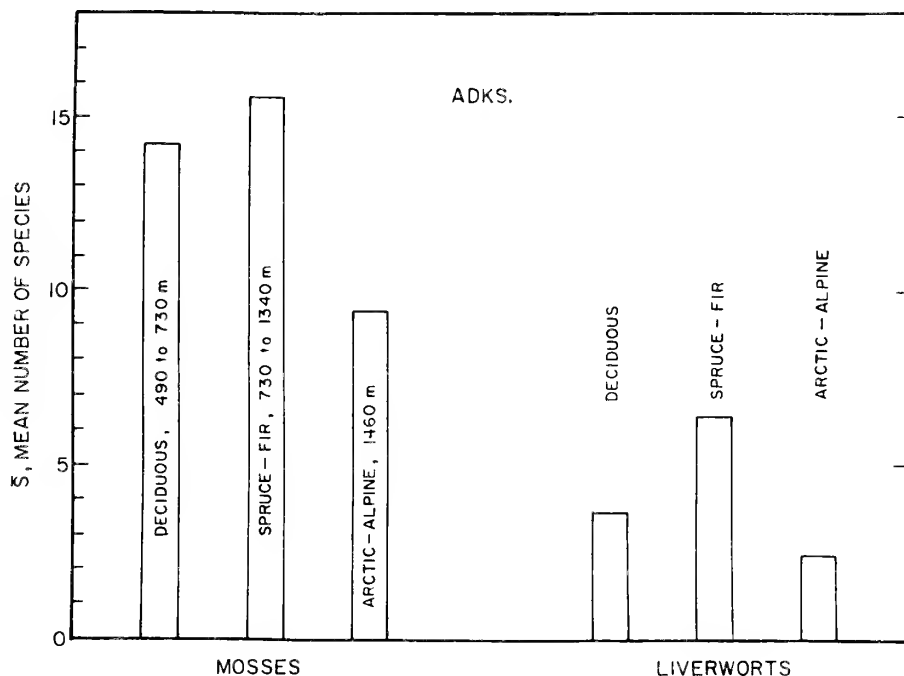
(photo by A. B. Wellborn)

Bryophyte-lichen mat over rock, arctic-alpine zone, Whiteface Mountain.

both in numbers of species and in dominance relationships. Evenness (J') varies from 0.25 to 0.80 for two summit quadrats with almost the same number of species ($S = 9,8$) resulting in diversity indices (H') of 0.55 and 1.66, respectively. The bryophytes are important members of the plant communities on the summit is shown by the fact that the percent of bryophyte cover averages 20 percent.

Ampersand Mountain also shows little change in diversity (H') with elevation, except that the highest diversity occurs at 1600 ft (940 m), an elevation where there is mature hemlock-northern hardwoods forest. Species richness (S) is similar to that of Whiteface quadrats at the same elevations, and is even higher at 2800 ft (850 m). H' values are lower than on Whiteface, however, because of high dominance,

FIGURE 4 Changes in mean species richness (S) of mosses and liverworts with elevation and forest type for Whiteface and Ampersand Mts.



especially at 2400 ft (730 m) and 2800 ft (850 m), both of which are in the spruce-fir zone.

Figure 4 shows changes in species richness (S) with elevation for mosses and liverworts separately. (Data for Whiteface and Ampersand Mountains are combined.)

One can see that for mosses little difference exists between the deciduous and the spruce-fir forest. Mean species richness (S), however, decreases greatly from the spruce-fir to the arctic-alpine zone. The maximum number of species drops also, from 20 to 10. For liverworts, however, mean species richness (S) increases significantly between deciduous and spruce-fir forest (see fig. 4), from a maximum of six in the deciduous to 11 per quadrat in the spruce-fir. Higher humidity, lower light intensity and persistent snow cover may all contribute to the higher liverwort diversity, especially under the pure *Abies balsamea* at 4400 ft (1340 m). The summit quadrats show the lowest mean number of species with few or no liverworts in the drier, rockier quadrats. Several liverwort species, however, often with relatively high cover value, are found in wetter, more protected parts of the summit area. Such liverworts as *Gymnocolea inflata*, *Anastrophyllum michauxii*, *Lophozia ventricosa*, *Ptilidium ciliare* and *Scapania nemorosa* add considerably to the diversity of arctic-alpine quadrat 21, just northeast of the summit.

Changes in Species Composition with Elevation

The original hypothesis, that bryophyte diversity is higher when a greater range of elevation is included in the analysis, was tested and appears to be tenable for the State as a whole. This is based on the results of the multiple regression analysis, for the elevation range of the Adirondack study, 1600 to 4800 ft (490 to

1460 m). The hypothesis assumes that species composition changes along this gradient. Two techniques of direct gradient analysis (Whittaker, 1968, 1970) were used to test this hypothesis. Since the first of these involved using a similarity value for comparison of species composition between quadrats at different elevations, the results of the comparison of four such similarity measures are presented first.

The four methods used to compare species composition were Sørensen's Q.S., Percent Similarity, and Sørensen's using only those species having at least five percent cover and one percent cover, respectively (see Analysis of Data section). I compared these four methods, using data from all three areas and all five plant types. I also made comparisons for various combinations of plant types, for example, shrubs, seedlings, and ground flora. Results presented here, however, refer to bryophytes on Whiteface and Ampersand Mountains, unless otherwise stated. Percentage Similarity and Sørensen's Q.S. values for all combinations of Adirondack quadrats are shown in table 2. Table 3 below shows correlation coefficients between the methods.

TABLE 3

Similarity Methods Compared	Corr. Coeff.
Percentage Similarity and Sørensen's Q.S.	0.79
Percentage Similarity and Sørensen's (.01)	0.85
Percentage Similarity and Sørensen's (.05)	0.87

Correlation coefficients among these indices for trees, shrubs, and tree seedlings were equally high whereas those for ground flora were somewhat lower. Correlation (0.87) is especially high between Percentage Similarity and Sørensen's (.05), in which species with less

SORENSEN INDICES (TOP RIGHT) AND PERCENTAGE OF SIMILARITY (BOTTOM LEFT) BETWEEN PLOTS

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.	21.	22.	23.	24.	25.
1	.000	.421	.341	.439	.263	.378	.238	.263	.267	.227	.154	.298	.226	.286	.250	.178	.263	.279	.158	.314	.000	.057	.054	.063	.000
2	.289	.000	.485	.485	.600	.483	.294	.267	.378	.389	.258	.256	.311	.412	.375	.324	.333	.229	.200	.326	.000	.074	.069	.083	.000
3	.208	.374	.000	.556	.424	.438	.378	.242	.400	.462	.412	.333	.333	.432	.400	.400	.364	.316	.242	.478	.059	.133	.125	.148	.077
4	.185	.279	.530	.000	.545	.500	.378	.182	.350	.359	.353	.238	.250	.432	.514	.400	.424	.263	.303	.478	.059	.133	.063	.074	.000
5	.104	.310	.227	.182	.000	.483	.294	.400	.486	.333	.323	.410	.444	.529	.438	.432	.533	.343	.400	.465	.000	.148	.069	.083	.000
6	.163	.312	.194	.238	.284	.000	.242	.207	.278	.400	.200	.263	.273	.424	.323	.278	.483	.235	.207	.333	.000	.154	.071	.087	.000
7	.136	.357	.365	.365	.150	.429	.000	.059	.341	.500	.743	.093	.204	.316	.500	.293	.353	.256	.118	.340	.057	.129	.121	.214	.074
8	.043	.038	.039	.024	.359	.269	.003	.000	.432	.111	.065	.513	.489	.294	.188	.270	.267	.457	.400	.372	.065	.074	.138	.083	.000
9	.092	.125	.119	.125	.182	.239	.220	.491	.000	.233	.316	.348	.385	.439	.359	.364	.378	.429	.324	.520	.105	.118	.167	.065	.000
10	.157	.271	.322	.298	.167	.227	.332	.003	.078	.000	.541	.133	.196	.350	.421	.279	.333	.146	.111	.286	.054	.061	.114	.200	.069
11	.120	.253	.287	.315	.115	.199	.392	.003	.091	.702	.000	.100	.174	.229	.424	.263	.387	.222	.129	.318	.063	.071	.133	.240	.083
12	.016	.086	.019	.033	.441	.230	.003	.434	.151	.008	.004	.000	.704	.419	.293	.348	.308	.500	.359	.462	.100	.167	.105	.061	.063
13	.010	.033	.057	.040	.090	.098	.023	.136	.077	.039	.020	.313	.000	.490	.255	.462	.400	.480	.400	.483	.087	.143	.182	.103	.053
14	.132	.253	.410	.300	.314	.257	.276	.083	.144	.246	.237	.102	.101	.000	.444	.585	.647	.462	.471	.596	.057	.258	.061	.000	.000
15	.145	.367	.360	.342	.259	.426	.511	.007	.088	.328	.322	.017	.042	.504	.000	.462	.438	.270	.188	.489	.182	.138	.194	.154	.080
16	.030	.149	.221	.159	.252	.199	.129	.183	.233	.123	.095	.123	.094	.496	.339	.000	.649	.571	.378	.640	.316	.353	.389	.258	.200
17	.047	.113	.123	.175	.173	.267	.143	.187	.187	.121	.155	.189	.159	.387	.182	.304	.000	.514	.400	.605	.194	.296	.276	.250	.174
18	.033	.145	.248	.118	.256	.169	.130	.245	.130	.097	.094	.293	.194	.282	.151	.240	.457	.000	.629	.625	.222	.375	.235	.138	.071
19	.024	.031	.074	.037	.107	.089	.013	.156	.098	.013	.013	.146	.173	.115	.019	.092	.561	.607	.000	.512	.129	.222	.069	.000	.000
20	.045	.118	.120	.173	.198	.268	.109	.243	.271	.065	.079	.243	.178	.313	.144	.292	.427	.375	.341	.000	.227	.200	.190	.162	.111
21	.000	.000	.002	.001	.000	.000	.001	.005	.010	.004	.027	.020	.009	.029	.005	.227	.039	.059	.030	.033	.000	.429	.600	.320	.333
22	.004	.007	.005	.010	.008	.010	.011	.007	.011	.003	.003	.022	.015	.042	.011	.057	.237	.281	.228	.062	.354	.000	.385	.190	.200
23	.001	.008	.010	.008	.003	.008	.009	.007	.016	.012	.003	.020	.011	.028	.012	.074	.047	.060	.028	.039	.347	.195	.000	.522	.455
24	.001	.001	.002	.001	.001	.001	.004	.001	.001	.006	.006	.006	.006	.000	.001	.014	.008	.007	.000	.003	.263	.560	.253	.000	.824
25	.000	.000	.002	.000	.000	.000	.001	.000	.000	.004	.027	.016	.005	.000	.001	.072	.011	.018	.000	.003	.156	.041	.199	.161	.000

CORRELATION COEFFICIENT BETWEEN SORENSON INDEX AND PERCENTAGE STABILITY = .754



(photo by A. B. Wellborn)

Pleurozium schreberi, dominant moss of the forest floor, spruce-fir zone, Whiteface Mountain (see fig. 8).



(photo by A. B. Wellborn)

(closeup of above)

than 5 percent cover value were eliminated. The Percentage Similarity measure not only stresses dominance but also effectively ignores species of low cover value. These species are not necessarily rare, however; *Tetraphis pellucida*, for example, occurs in 12 different quadrats, but in only three of these is its relative cover value greater than five percent. This moss is an important member of the bryophyte community, occurring very regularly on decaying stumps, but rarely in large quantities since its substrate is limited. Thus the Percentage Similarity index may ignore a frequent species with a highly specific niche but low cover value. Sørensen's index, on the other hand, is said to overvalue rare species. This is not true where the rare species differ in the quadrats compared; different rare species lower the Sørensen index, but have no effect on Percentage Similarity.

The relatively high correlation (0.79) between Sørensen's Q.S. and Percentage Similarity arises from the fact that, in general, bryophytes do not show very high dominance; where dominance is not unusually high, the two methods give similar results. High dominance exists in two very different habitats in this study. In the spruce-fir forest, particularly at higher elevations under fir, carpets of *Pleurozium schreberi* accounted for up to two-thirds of the total bryophyte cover. Percentage Similarity is unusually high here (0.784). Similar unispecies bryophyte carpets occur in conifer forest elsewhere. For example, *Hylocomium splendens* forms such carpets in northern Sweden as does *Tomenthypnum nitens* in western Alberta. Unusually high dominance also occurs in some of the arctic-alpine quadrats, particularly those in which conditions are particularly rigorous. A comparison of arctic-alpine quadrats 22 and 24 in table 2, for example, shows a Sørensen's Q.S. of 0.190, but Percentage Similarity of 0.560. The high Percentage Similarity results from the dominance of one species, *Polytrichum strictum* (formerly *P. juniperinum* var. *gracilius*) which comprises 55 percent and 84 percent of the total bryophyte cover in the two quadrats. On the other hand, a comparison of quadrat 24 with another arctic-alpine quadrat, 25, gives a very different result, Sørensen's 0.824, Percent Similarity only 0.161. In this case, seven of the ten species are found in both quadrats, but the dominance relationships in the two quadrats are completely different.

These indices are used in examining the following important aspects of community structure:

- 1) Which species have physiological tolerances that enable them to grow at certain elevations?
- 2) How is niche space divided up within a community?



(photo by A. B. Wellborn)



(photo by N. G. Slack)



(photo by N. G. Slack)

TOP LEFT:

Ground flora, Ampersand Mountain, with *Aralia nudicaulis*, *Oxalis montana*, seedlings of *Acer saccharum*, *A. spicatum* and *A. pensylvanicum*.

TOP RIGHT:

***Acer saccharum*, dominant canopy tree, deciduous forest, Whiteface Mountain.**

ABOVE:

***Acer pensylvanicum*, common understory tree, deciduous forest on Whiteface and Ampersand Mountains.**

LEFT:

***Abies balsamea* and *Picea rubens*, dominants of coniferous forest, upper slopes, Whiteface Mountain.**



(photo by N. G. Slack)

Sørensen's index, which "counts" species if they are present even in small quantities, gives better answers to the first question. Percent Similarity, stressing dominance relationships, gives better answers to the second. Therefore, I have retained both of these indices in showing changes in species composition with elevation (tables 2 and 3; figs. 5 and 6). Question 1 is discussed further below. Question 2, including dominance-diversity relationships and the division of niche space is discussed in a later section.

Both the Sørensen and Percent Similarity values have been used for comparison at the same elevation in pairs. Table 4 shows values for some elevations. (For the complete matrix for all Adirondack quadrats, see table 2.) It can be seen in table 4 that comparisons between quadrats at 1600 ft (490 m), numbers 1-4, give high values whether compared on the same mountain or between mountains. At this elevation, a relatively mature deciduous forest dominated by *Acer saccharum* occurs on both mountains. At 2400 ft (730 m), comparisons of quadrats on the same mountain (8 and 9; 10 and 11) show high similarity values; comparisons between mountains (quadrats 9 and 10; 8 and 11)

show very low values. The transition between deciduous forest and spruce-fir forest occurs at somewhat different elevations on different mountains in the Adirondacks, and even on different sides of the same mountain. At 2400 ft (730 m) there is already spruce-fir on Ampersand; on Whiteface, at least on the northeastern slope used in this study, there is still deciduous forest. The forest type is thus shown to be significant in terms of species composition of bryophytes in the ground layer.

Table 4 also shows comparisons within the spruce-fir and arctic-alpine groups of quadrats, and between quadrats of these two groups. In almost all cases within-group similarity is much higher than between-group similarity in the arctic-alpine area and those in the spruce-fir zone. The lower values for some spruce-fir quadrats using Percent Similarity results from the high dominance of one species, *Pleurozium schreberi*, in these quadrats, as pointed out above. Notable also is the complete lack of similarity (0.0) of bryophytes with either index in some comparisons of spruce-fir and arctic-alpine vegetation. (See quadrats 19 and 24, and 19 and 25 compared in table 2 and at the bottom of table 4).

TABLE 4
Bryophytes—Species Composition vs. Elevation
Ampersand (A) and Whiteface (W) Mountains

Zone	Mountains compared	Elevations compared	Q.S.	% Sim.
<i>Deciduous</i> (Quadrats 1-4)	A-A	490 m	0.421	0.289
	W-W	490 m	0.556	0.530
	A-W	490 m	0.485	0.374
	A-W	490 m	0.485	0.279
<i>Deciduous to Spruce-Fir Transition</i> (Quadrats 8-11)	A-A	730 m	0.431	0.491
	W-W	730 m	0.541	0.702
	A-W	730 m	0.111	0.003
	A-W	730 m	0.065	0.078
<i>Spruce-Fir</i> (Quadrats 18-20)	W-W	1220-1340 m	0.512	0.341
	W-W	1100-1340 m	0.625	0.375
	W-W	1100-1220 m	0.629	0.607
<i>Arctic-Alpine</i> (Quadrats 21-25)	W-W	1460 m	0.429	0.354
	W-W	1460 m	0.600	0.347
	W-W	1460 m	0.190	0.560
	W-W	1460 m	0.824	0.161
<i>Spruce-Fir-Arctic-Alpine</i> (Quadrats 18, 19, 21, 24, 25)	W-W	1220-1460 m	0.221	0.059
	W-W	1340-1460 m	0.129	0.030
	W-W	1340-1460 m	0.000	0.000

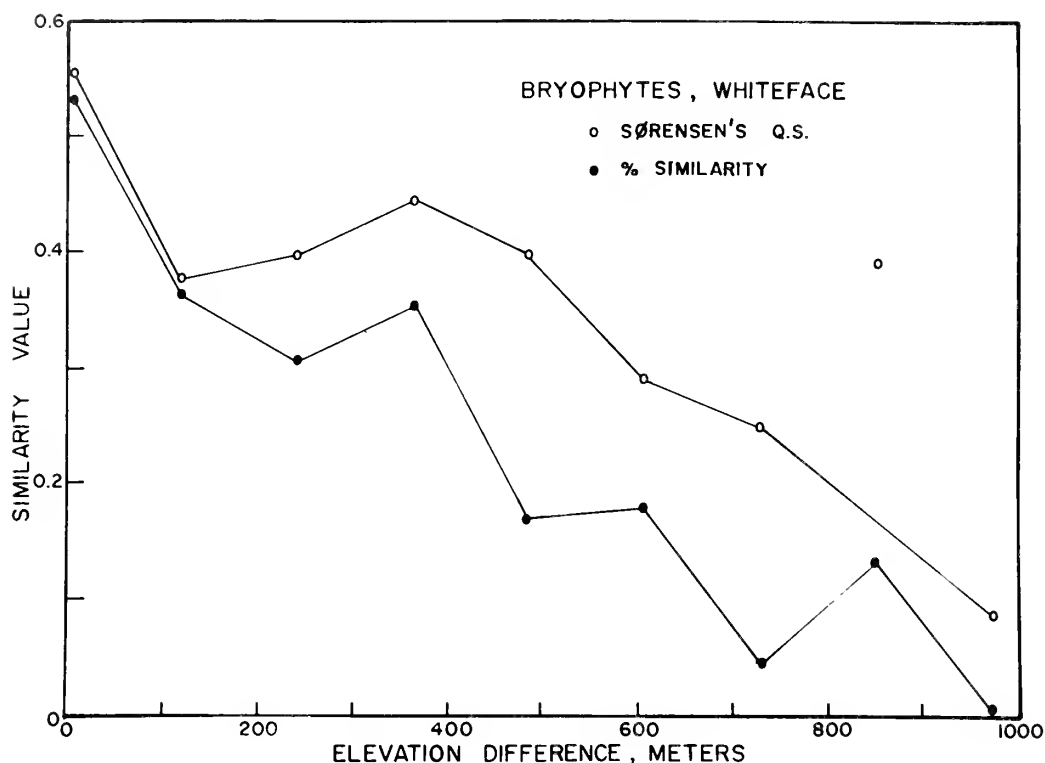


FIGURE 5 Changes in bryophyte species composition with increasing separation in elevation on Whiteface Mt.

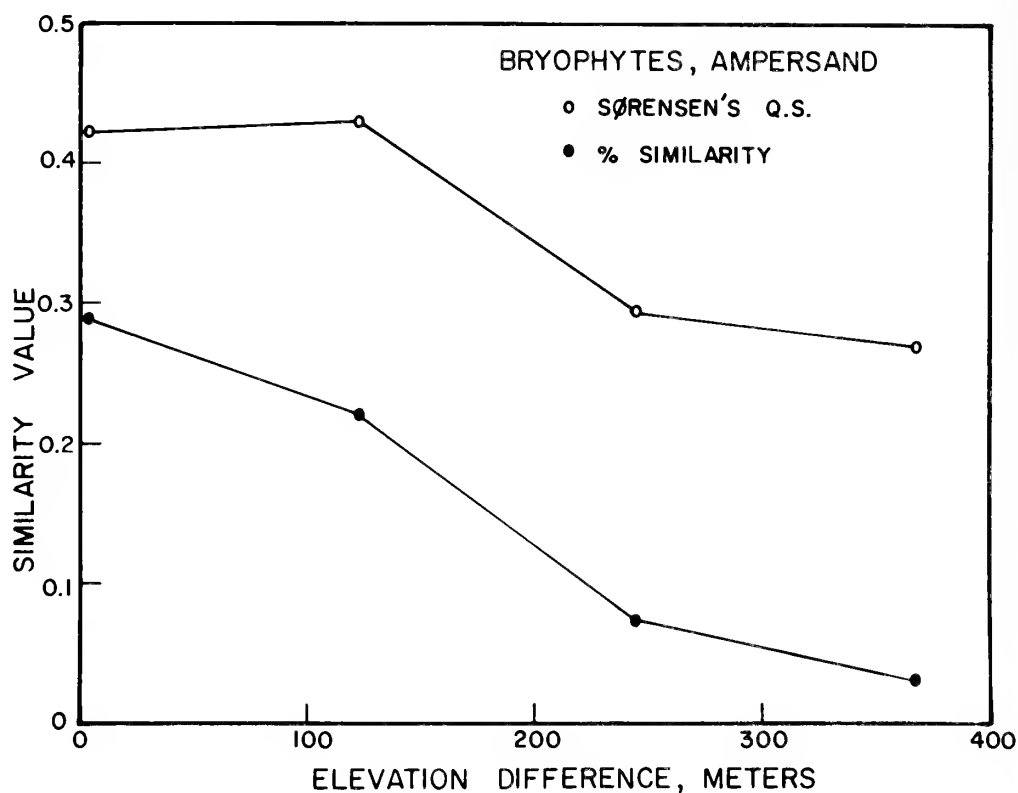


FIGURE 6 Change in bryophyte species composition with increasing separation in elevation on Ampersand Mt.

Figures 5 and 6 show changes in bryophyte species composition with increasing separation in elevation. The 0.0 separation point for both Whiteface (fig. 5) and Ampersand (fig. 6) is at 1600 ft (490 m). Thus on Whiteface (see fig. 5), the quadrats at 490 m show a

similarity of over 0.5, whichever index is used. In the spruce-fir zone, 600 m higher, the similarity with the 490 m quadrats is about 0.3 using the Sørensen, and about 0.2 using the Percent Similarity. The arctic-alpine quadrats at almost 1000 m separation from the

lowest quadrats used in this study show similarities of less than 0.1 using either index. The fact that it is not 0.0 shows that some species do occur in both the lowest and highest elevations on Whiteface, examples being *Ptilidium pulcherrimum* and *Dicranum montanum* (of fig. 12). A general decrease in similarity of species composition is seen on both mountains as the distance from the lowest quadrats increases. A sharp decrease in similarity is seen at about 250 m separation on Ampersand Mountain (fig. 6), which is the region of transition from deciduous to spruce-fir forest. On Whiteface, the greatest change occurs between 370 and 490 m separation, again at the deciduous forest to spruce-fir transition. Although forest type has been shown to be an important determinant of bryophyte species composition, Sørensen values of 0.3 or more indicate the presence of some of the same bryophyte species in both deciduous and spruce-fir forest. Many species (cf. figs. 9–12) are found in both forest types, for example, *Dicranum scoparium*, *Polytrichum ohioense*, *Plagiothecium laetum*, *Hypnum pallescens*, *Ptilidium pulcherrimum*, and even *Brotherella recurvans*, usually thought of as a spruce-fir indicator species. Like *Brotherella*, the relative cover values of most of the species change with elevation, as discussed in the following section.

Distribution Patterns of Bryophytes in Relation to Elevation

Correlation coefficients between relative cover (percent of total cover of all bryophytes) and elevation for each bryophyte species were computed. All those species which had significant correlation coefficients as well as all those that were present in at least five quadrats were used to study patterns of distribution of species on Whiteface and Ampersand Mountains. Bar graphs were made for each of these species for all quadrats on both mountains. Figures 7 to 12 show the resulting distribution patterns for representative species. The following distribution patterns were found:

- arctic-alpine (fig. 7)
- spruce-fir and arctic-alpine (fig. 8)
- entirely or predominantly spruce-fir (fig. 9)
- deciduous and spruce-fir (fig. 9)
- predominantly deciduous (fig. 11)
- deciduous, spruce-fir, and alpine (fig. 12)

In figure 7, all five arctic-alpine quadrats are shown separately so that dominance relationships in the various quadrats can be compared. Although all the bryophytes shown in figure 7 are species of specialized habitats and, to varying extents, extreme conditions, they are not all limited to arctic-alpine habitats. *Polytrichum piliferum*, for example, is found in dry, ex-

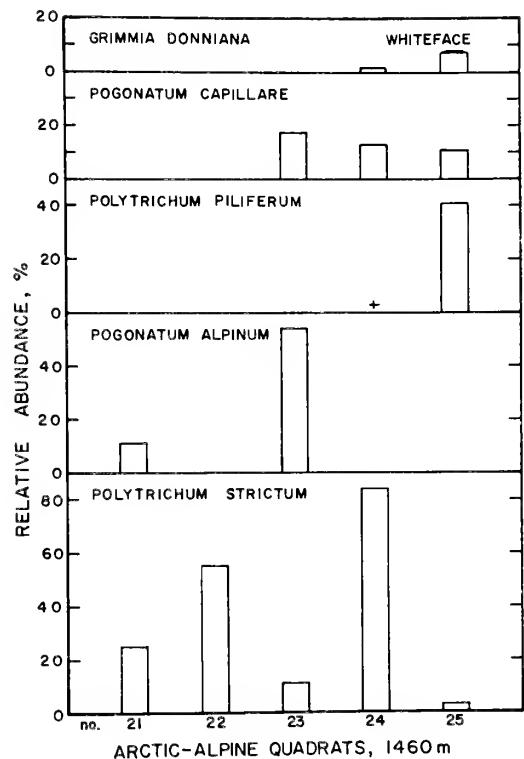


FIGURE 7 Relative abundance of species restricted to the arctic-alpine zone on Whiteface Mt.

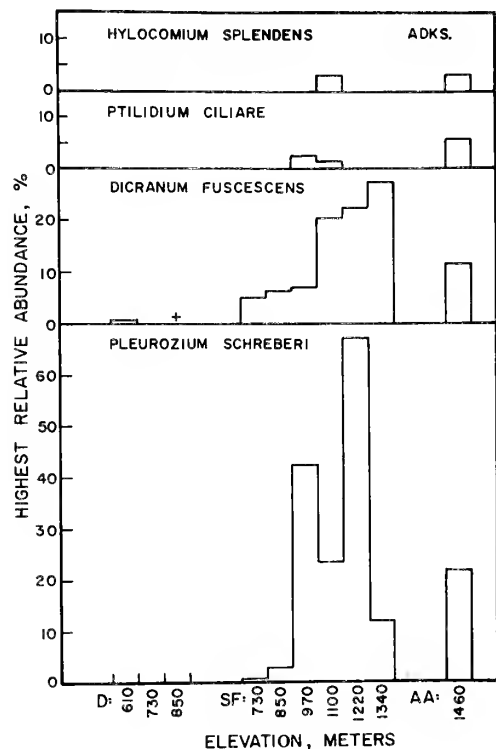


FIGURE 8 Spruce-fir and arctic-alpine

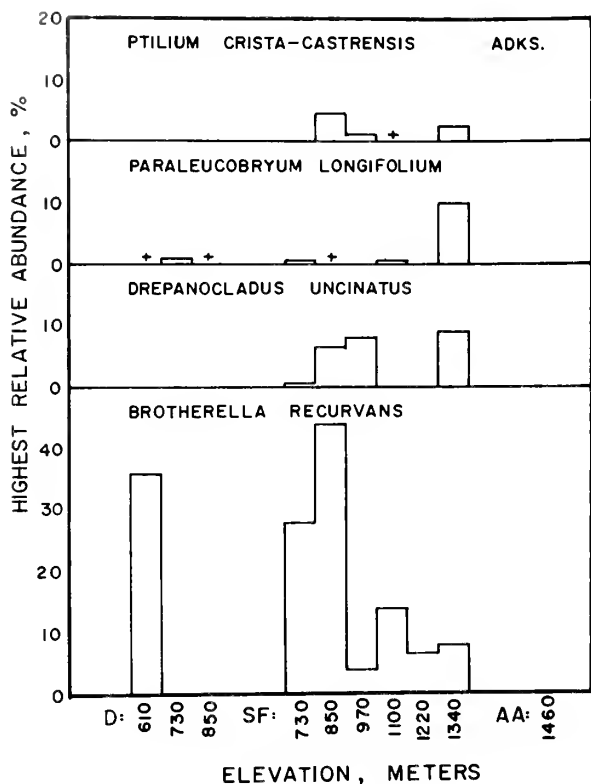


FIGURE 9 Entirely or predominantly spruce-fir

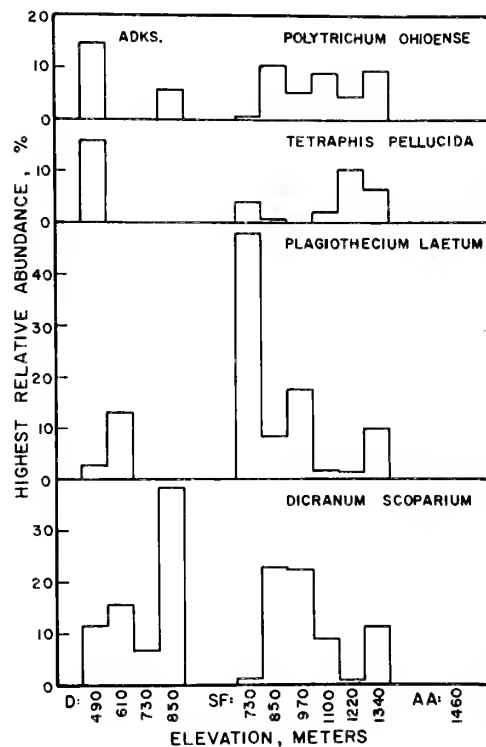


FIGURE 10 Deciduous and spruce-fir

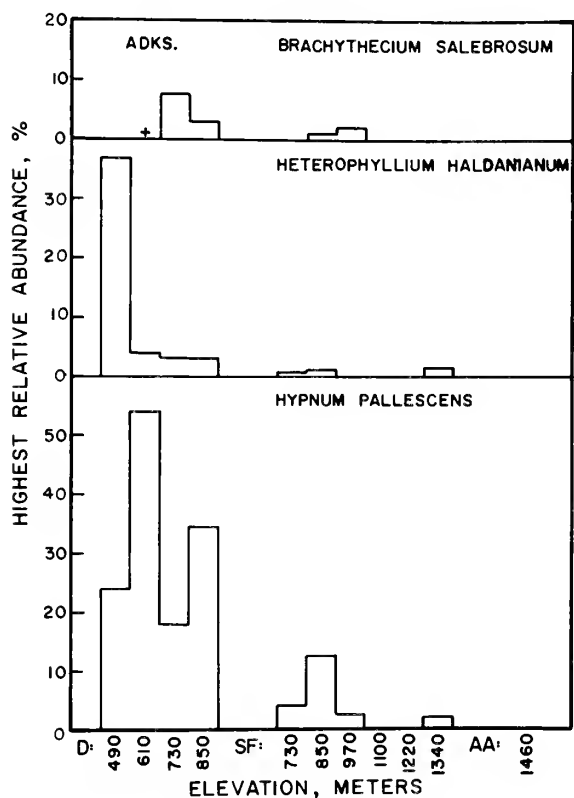


FIGURE 11 Predominantly deciduous

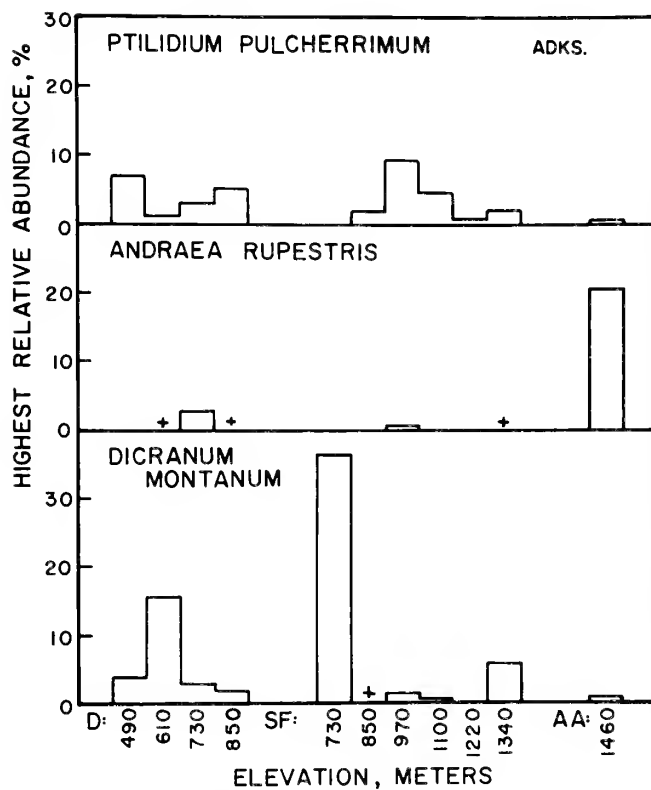


FIGURE 12 Deciduous, spruce-fir, and alpine

FIGURES 8-12 Distribution patterns for representative species of bryophytes on Whiteface and Ampersand Mts.

posed nonalpine areas as well. It is noteworthy that four out of five of these species belong to one family, the Polytrichaceae. The fifth, *Grimmia donniana* is restricted to this zone, but *Grimmia apocarpa* is also found here. This species and *Andreaea rupestris* are found both in the arctic-alpine zone and at lower elevations where suitable rock substrates occur. The Polytrichaceae and Grimmiaceae (including *Racomitrium heterostichum*, also found at high elevations on Whiteface), as well as *Andreaea*, show a variety of adaptations to high winds, drying, and other aspects of exposure. These include lamellae, hair points, and a clumped or turfed growth form. Other bryophytes found only in the arctic-alpine quadrats, but in more moist habitats, were, *Sphagnum russowii*, *Calliergon stramineum*, *Anastrophyllum michauxii*, and *Gymnocolea inflata*.

Many lichens, particularly crustose lichens, also show the same pattern of distribution. Lichens were noted but not included in the present study. At lower elevations, they form a very minor component of the plant communities except as epiphytes. Above timberline in the arctic-alpine summit area, however, they become a major component, both as fruticose forms, largely *Cetraria* and *Cladonia* species, on the ground, and crustose species on rocks. In one summit quadrat, I distinguished fifteen species of lichens, giving a higher species richness (S) than for either bryophytes or vascular plants. Further work on plant diversity in this zone should include lichens.



(photo by A. B. Wellborn)

Polytrichum piliferum, showing hair points, near summit, Whiteface Mountain.



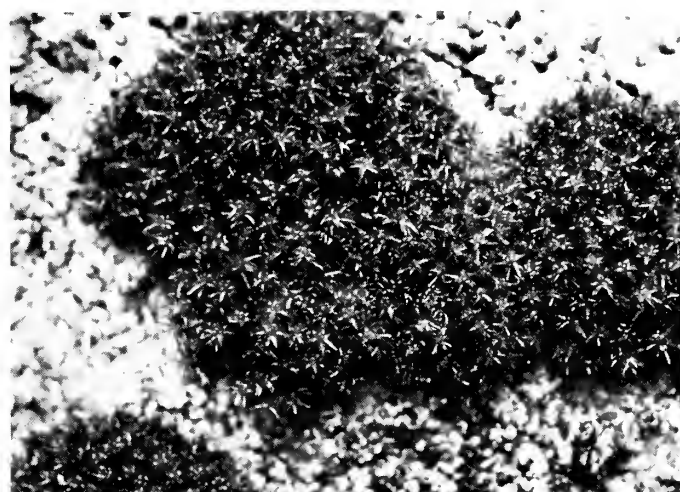
(photo by A. B. Wellborn)

Dicranum scoparium, a dominant moss of deciduous forests, also found in spruce-fir forests (see fig. 10).



(photo by A. B. Wellborn)

Andreaea rupestris, characteristic moss of arctic-alpine zone, also found on suitable rock outcrops at lower elevations.



(photo by A. B. Wellborn)

Andreaea rupestris with crustose lichens on rock face near summit, Whiteface Mountain.

Species characteristics of the spruce-fir zone and also found in the arctic-alpine area are shown in figure 8. One of these, *Ptilidium ciliare*, reaches its highest cover value in the latter area where it grows among lichens, particularly *Cetraria islandica*. (It is found at altitudes of at least 4500 ft in the krummholz, associated with *Polytrichum juniperinum*.) Some of the predominantly spruce-fir species are shown in figure 9; two of these, *Ptilium crista-castrensis* and *Drepanocladus uncinatus*, were found only in spruce-fir quadrats, though both were occasionally found at lower elevations. Two very characteristic species of this zone, *Bazzania trilobata* and *Brotherella recurvans* (fig. 9) were found also in deciduous forest quadrats.

Several other species were restricted to the spruce-fir zone, but found only in small quantities. One of these, *Isopterygium distichaceum* (formerly *I. subfalcatum*), is of particular interest because it does not appear in the New York State checklist (Ketchledge, 1957) for the Adirondacks, and there was only one report for the whole State at that time. Six collections were made in this study, at 2400 ft (730 m) and 2800 ft (850 m) on Ampersand and at 4000 ft (1220 m) on Whiteface, all within the spruce-fir zone.

Representative species present in both deciduous forest and the spruce-fir zone, the most common distribution for bryophytes in the study, are shown in figures 10 and 11. Of these, probably only *Plagiothecium laetum* is more characteristic of spruce-fir than of deciduous forest. Two other species of *Hypnum*, in addition to *H. pallenscens* (including *H. reptile* Michx of the New York checklist, fig. 11), *Hypnum lindbergii* and *H. imponens* were also found predominantly in the deciduous forest quadrats. Of the eight species of *Brachythecium* found, six, including *B. salebrosum* (fig. 11) had distributions largely in deciduous forest. Two species, *B. curtum* and *B. reflexum*, grow in both deciduous and spruce-fir forest.

A few species occur throughout the elevation range wherever conditions are suitable. These include species growing on rock, such as *Grimmia apocarpa* and *Andreaea rupestris*, as noted above, and those growing on wood such as *Dicranum montanum* and *Ptilidium pulcherrimum* (fig. 12.). Weedy species such as *Dicranella heteromalla* and *Pohlia nutans* occur over the whole elevation range, but are uncommon in mature forest quadrats, although common along the trails and in other open, disturbed areas even above timberline.

It is clear that differing distributions of the bryophyte species over the elevation range used in this study add to the overall bryophyte diversity. Both species presence and relative density (cover) change with elevation for the great majority of species. Differing physiological tolerances and competition among species are probably both involved; only an experi-



(photo by A. B. Wellborn)

Polytrichum juniperinum and *Ptilidium ciliare* bryophyte mat, characteristic of krummholz zone, Whiteface Mountain.

mental approach could distinguish these two causes of change in species along the elevation gradient. Tolerance and competitive ability are, of course, related. Species only moderately tolerant of arctic-alpine environmental conditions are unlikely to be good competitors in that zone. Competition, both among bryophyte species and between bryophytes and vascular plants, is discussed in a later section.

The Relation Between Total Bryophyte Cover and Diversity

In figure 13, the actual percent cover of Adirondack bryophytes is shown graphically with diversity (H') of bryophytes at each elevation. The cover value is the percent of each quadrat covered by all bryophytes. It varies in the Adirondack quadrats from 0.6 to 44.3 percent. It can be seen that the cover value, which indicates the relative importance (incorporating both density and basal area) of bryophytes in the whole plant community, increases rapidly where the spruce-fir zone is reached. This occurs at a lower elevation on Ampersand than on Whiteface, as noted above. Diversity, on the other hand, did not change greatly with elevation, at least below 4000 ft (1220 m). The arctic-alpine quadrats also have high cover values, often 20 percent or higher except in unstable rockslide areas, but with relatively low diversity compared to lower elevations. Diversity is highest at 1600 ft (490 m) on Ampersand, where cover values reach a maximum of only 2.2 percent! Thus the total cover of bryophytes is not correlated in the Adirondack quadrats with diversity, nor is any such correlation found when species richness (S) is used instead of Shannon diversity index.

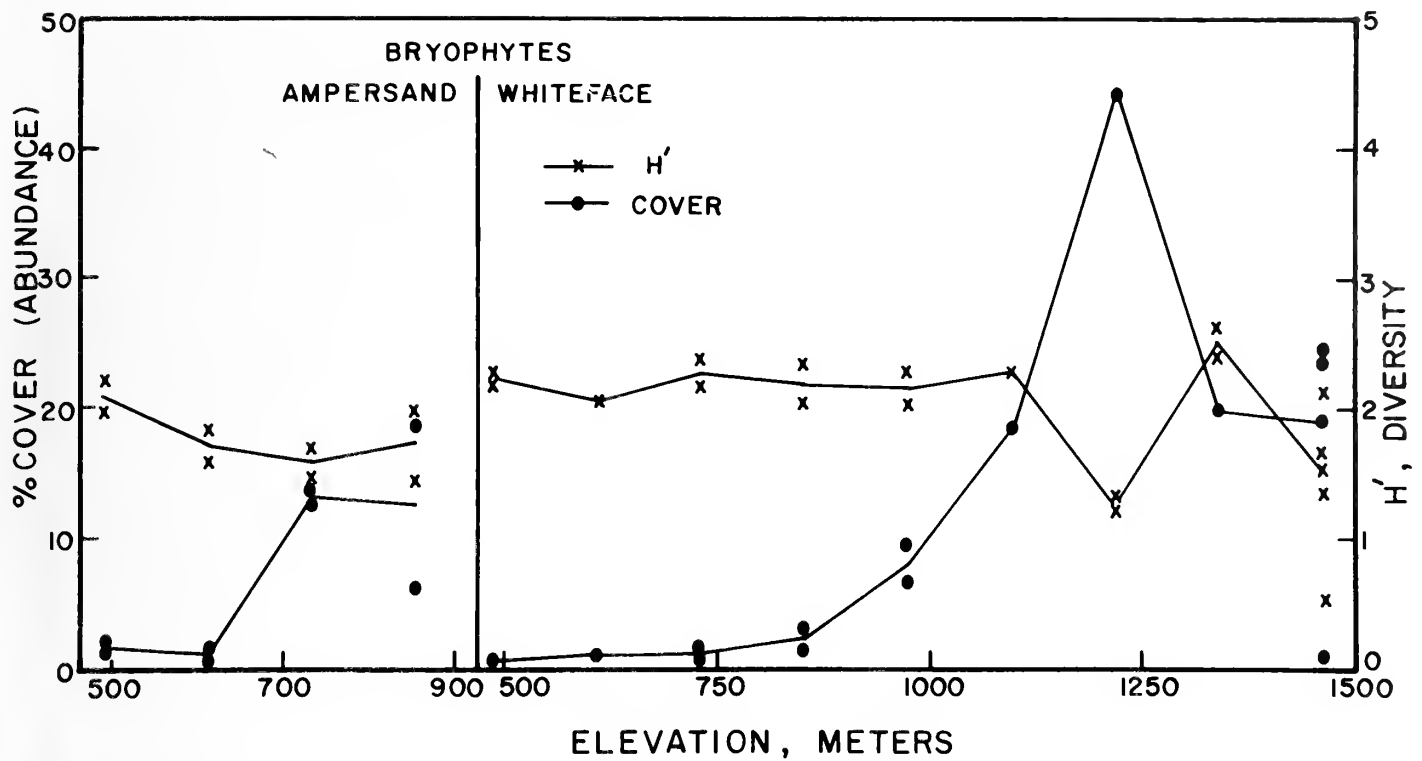


FIGURE 13 Percent cover bryophytes and diversity (H') at each elevation at Ampersand and Whiteface Mts.

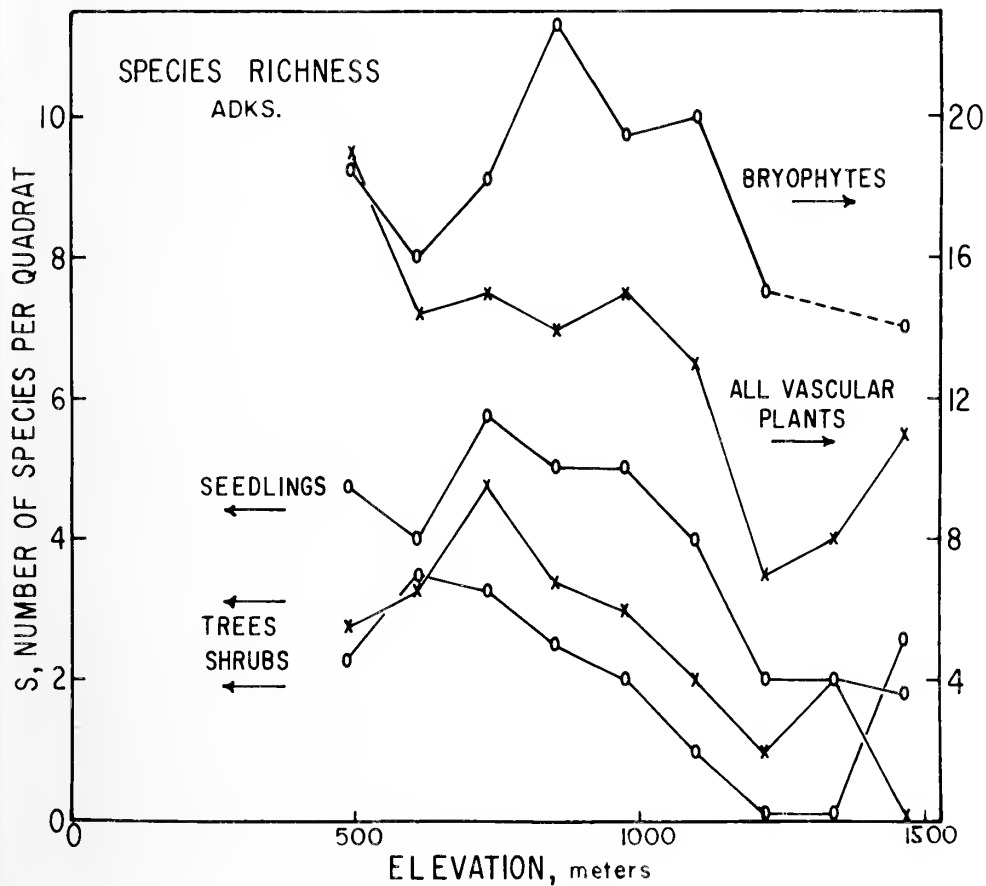


FIGURE 14 Changes in species richness (S) with elevation for: bryophytes, all vascular plants, tree seedlings, trees, and shrubs at Whiteface and Ampersand Mts.

Within any one vegetation zone, however, diversity (H') and cover may be correlated. In the deciduous forest on Ampersand, diversity and cover values are as follows for the four quadrats:

% cover: 0.55	0.98	1.5	1.8
H' : 1.59	1.83	1.96	2.21

On Whiteface, however, the diversity values are all quite similar for the deciduous quadrats (2.0 to 2.38 for six quadrats) and there is no such direct relationship. The Kenrose Preserve data (see separate section below) do show positive correlation ($r = -0.63$) of total bryophyte cover and bryophyte diversity in the deciduous forest.

Bryophytes in Relation to Other Plant Strata

Figure 14 shows changes in species richness (S) with elevation on Whiteface and Ampersand for trees, shrubs, seedlings, and bryophytes. For clarity, ground flora is not shown separately here but is included in "all vascular plants." (It is shown separately in figure 15.) It can be seen that bryophytes show higher species richness than all vascular plants together except at 1600 ft (490 m) where they are about equal in numbers of species. Both trees and tree seedlings peak at about 2400 ft (730 m), where a variety of deciduous trees and seedlings occur together with a small admixture from the spruce-fir forest. The total number of vascular plant species, however, decreases with elevation, although there is a sharp increase at the summit. This increase results from a large number of shrub species such as *Vaccinium uliginosum* and *Ledum groenlandicum*, which only occur in the arctic-alpine zone in this study.

The number of species of bryophytes present within quadrats of one vegetation zone varied considerably. Within the larger forest types, such as spruce-fir, much variation exists. One can subdivide this type into a number of subtypes, based on relative dominance of red spruce and balsam fir. The presence of the latter depends on ground moisture as well as on elevation. Balsam fir becomes dominant at the higher elevations, but, even within pure balsam fir stands, the trees differ in age and density. Such structural differences within one forest type should be studied further in relation to bryophyte diversity. In some stands of fir, the presence of dead lower branches resulted in more light and lower humidity and a bryophyte layer on the forest floor quite different from that in other stands. At 4400 ft (1340 m) on Whiteface, where there is dense fir forest and very late snow cover, species richness of bryophytes and especially of liverworts, rises very sharply (see fig. 3). The high humidity in *Abies* stands, so dense that one can hardly stand up in these quadrats, is increased by the late snow melt, and



(photo by N. C. Slack)

Less mature deciduous forest with much *Betula papyrifera*, Whiteface Mountain; high bryophyte diversity was found here.

creates conditions favorable to many liverworts.

The deciduous forest stands also vary in species composition, in part a result of differences in maturity. The maximum number of bryophyte species was almost as high (25) in deciduous forest quadrats as in spruce fir (30) or in pure fir (28), in spite of the much greater cover of bryophytes under spruce and fir. Within the deciduous forest zone, a slightly higher maximum number of species occurred in the less mature deciduous forest with much *Betula papyrifera* (25) than in the mature sugar maple-beech forest (23). In each of the above forest types, the species composition differed. Thus the within-habitat (alpha) diversities for the different forest types add up to a high between-habitat (beta) diversity over the whole elevation range. This finding further corroborates the original hypothesis regarding species diversity and elevation range.

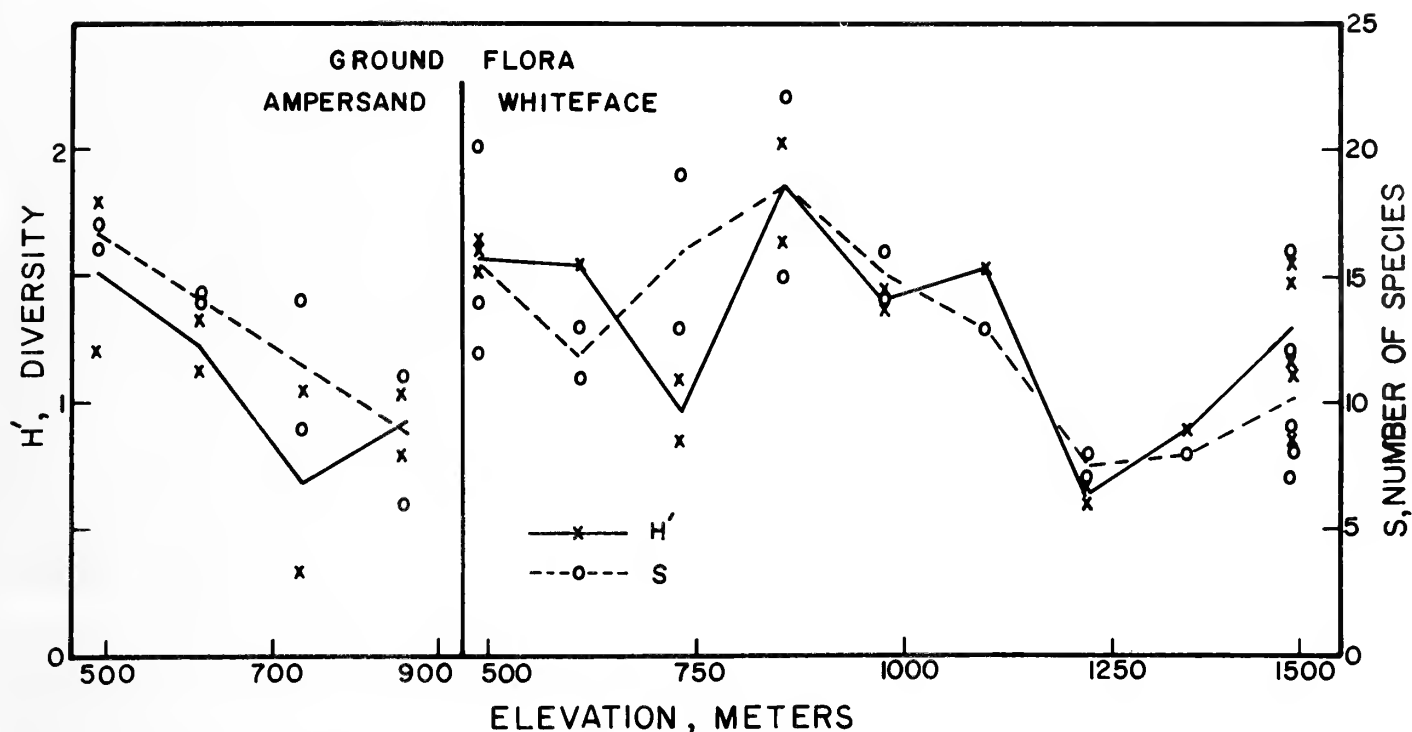


FIGURE 15 Changes in species richness (S) and diversity (H') for ground flora with changes in elevation at Ampersand and Whiteface Mts.



Oxalis montana, dominant herbaceous vascular plant in spruce-fir zone on Whiteface and Ampersand Mountains.

(photo by A. B. Wellborn)

Vascular ground flora was studied quantitatively in each of the quadrats (see field methods). When species richness (S) and diversity (H') are plotted for the ground flora in relation to elevation (fig. 15), no clear relationship is seen over the whole range of elevations on Whiteface. On Ampersand, with a more limited elevation range, both S and H' are seen to decrease with elevation; they are higher in the deciduous than in the spruce-fir forest. On Whiteface, high and low diversities were found in both forest types; factors other than elevation appear to be important in determining the number of species in the ground flora and their relative abundances. At 4000 ft (1220 m) a dominant herbaceous vascular plant, *Oxalis montana*, accounts for 82 to 85 percent of the ground flora density in these quadrats, and accounts for the low evenness values ($J' = 0.40, 0.36$). In these same quadrats, one bryophyte, *Pleurozium schreberi*, similarly accounts for a low J' and consequently low H' value for bryophytes as explained above.

As has already been seen for bryophytes, the species composition of the ground flora changes with elevation; also, the range of elevations adds to the diversity of the ground flora for the whole mountain. For example, at 4800 ft (1490 m), in the arctic-alpine quadrats, many plants appear that do not occur at lower elevations, even at 4400 ft (1340 m). These include *Agrostis borealis*, *Arenaria groenlandica*, *Carex bigelowii*, *C. brunnescens*, *Juncus trifida*, *Lycopodium selago*, *Potentilla tridentata*, *Scirpus caespitosus*, and *Solidago cutleri*. Thus, Sørensen and Percent Similarity values



(photo by N. G. Slack)

Lower layers in *Abies balsamea* forest, Whiteface Mountain, showing *Oxalis montana* and young balsam reproduction.

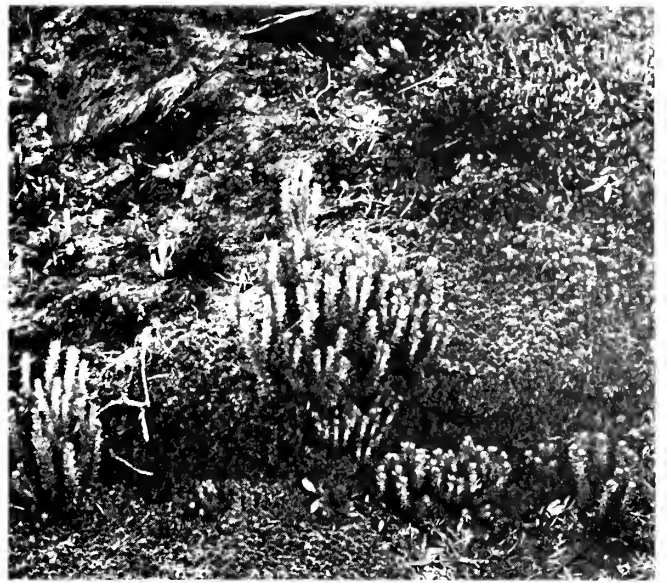


(photo by N. G. Slack)

Ground flora of transition zone, Whiteface Mountain, including *Cornus canadensis*, *Lycopodium lucidulum*, *Monotropa uniflora*, *Oxalis montana*, and the moss, *Dicranum scoparium*.



(photo by A. B. Wellborn)



(photo by A. B. Wellborn)



(photo by N. C. Slack)



(photo by A. B. Wellborn)

TOP LEFT:

Ground flora of deciduous forests, including *Medeola virginiana*, *Dryopteris spinulosa*, *Acer saccharum* and *A. pensylvanicum* seedlings.

TOP RIGHT:

Bryophyte community and *Lycopodium selago*, arctic-alpine zone, Whiteface Mountain.

ABOVE:

Ground flora of *Abies balsamea* forest including *Oxalis montana*, and mosses *Hylocomium splendens* and *Pleurozium schreberi*.

RIGHT:

Lycopodium selago with *Ledum groenlandicum* and *Cetraria islandica*, arctic-alpine zone, Whiteface Mountain.

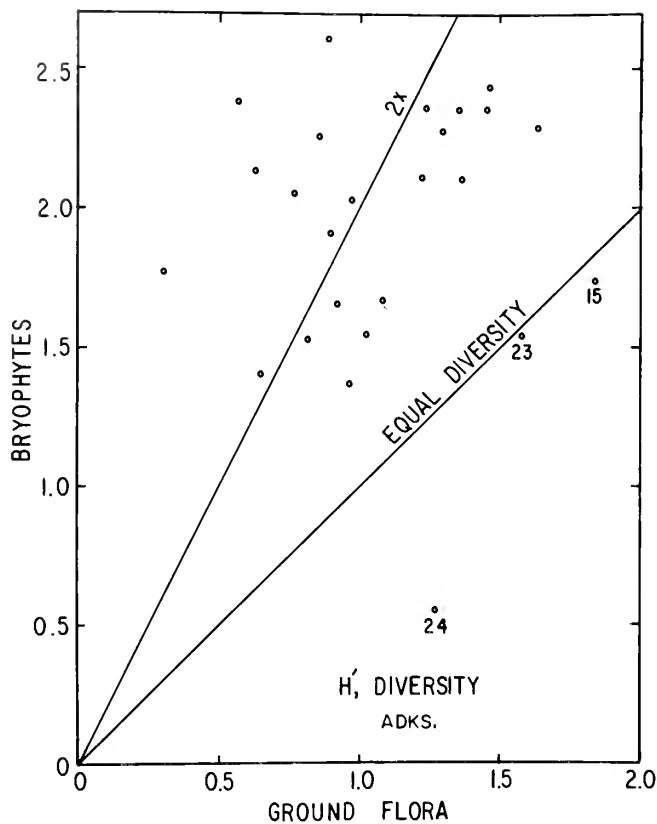


FIGURE 16 Bryophyte diversity (H') versus ground flora diversity (H') at Ampersand and Whiteface Mts.

between quadrats at 4400 ft and 4800 ft are very low (0.00 to 0.14). Similarly, some species occur in the deciduous forest quadrats but not at higher elevations. Thus, the ground flora showed patterns over the elevation gradient similar to those shown for bryophytes in figures 5 and 6 and 7 through 12.

The diversity (H') of the ground flora and that of shrubs is compared with that of bryophytes in figures 16 and 17. The shrub category included shrubby understory trees such as *Salix*. The large quadrat size (40 m²) makes comparison of these strata possible, but it is probably too small for reliable comparison with canopy trees. With the notable exception of quadrat 24, diversity (H') is approximately equal or higher for bryophytes than for the ground flora of shrubs. For almost all quadrats, it is considerably higher (see figs. 16 and 17). Even in arctic-alpine quadrat 24, the number of species of bryophytes (9) is higher than the number of species on the ground flora (5) or of shrubs (2), but the evenness component (J') is only 0.25, the lowest for bryophytes in the entire study. *Polytrichum strictum* accounts for more than 80 percent of the bryophyte cover in this quadrat.

I have compared the Adirondack data with those for other mountain areas such as the Great Smokies and the Rocky Mountains (Whittaker, 1956, 1967; Bliss,

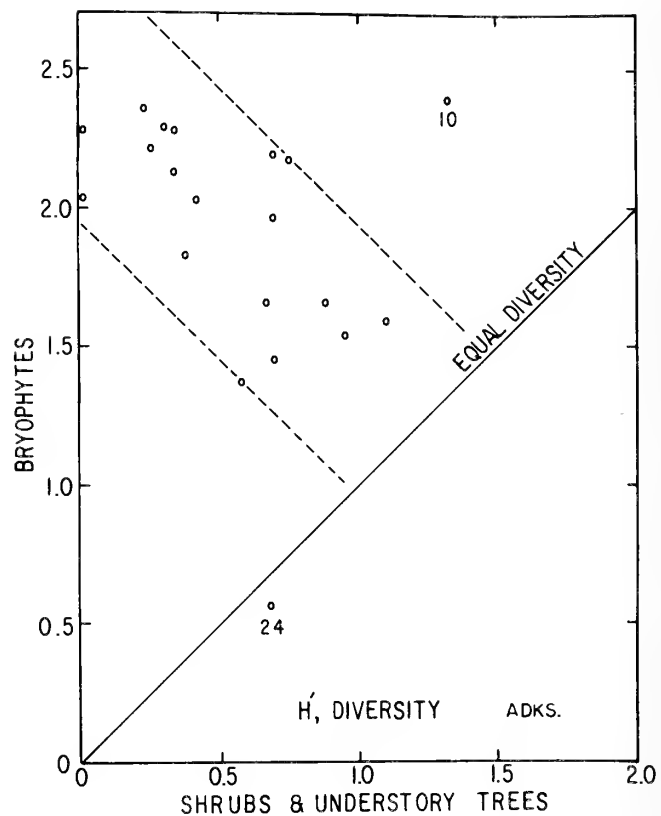


FIGURE 17 Bryophyte diversity (H') versus shrub diversity (H') for Ampersand and Whiteface Mts.

1963). The number of vascular plant species is lower in the Adirondacks than in the other areas, so that this high ratio of bryophytes to ground flora may not be a general one. It may, however, be characteristic of spruce-fir forest, in which low light levels and high humidity favor bryophytes over herbaceous vascular plants; more data are needed to resolve this question. In the Southern Blue Ridge of North Carolina, where I have also been working, species richness of both vascular plants and bryophytes is higher than in the Adirondacks, at least in deciduous forest. Within-habitat diversity of bryophytes and vascular plants has not yet been studied there, in a comparable way; therefore, further comparisons are not yet possible.

No particular effect of ground flora diversity on that of bryophytes can be seen in figure 16. Interactions are present, however. Apparent competition between an herbaceous vascular plant, *Oxalis montana*, and a bryophyte, *Pleurozium schreberi*, was noted in the quadrats at 4000 ft (1220 m); where *Oxalis* density was very high, the moss was absent or appeared dead. *Oxalis* seedlings had germinated in the *Pleurozium* carpet, however, and where the *Oxalis* was less dense, both occurred together. The moss can photosynthesize both early in the season before the *Oxalis* leaves expand and in early fall after they have been killed by

frost, to allow some seasonal variation in resource use. Here, the question of competition could be studied by removal of *Oxalis* and/or moss completely or to various density levels in different plots. Very little is known, however, about growth rates of bryophytes in nature. A one dm² plot of *Pleurozium* adjacent to quadrat 19 at 4000 ft (1220 m), which I removed, showed no sign of regrowth after more than a year, although surrounded by undisturbed *Pleurozium schreberi*.

Figure 17 does show an inverse relationship between bryophyte diversity (H') and shrub and understory tree diversity ($r = -0.31$). This may be the result of competition; with more shrub species there may be less light, less water, or less space available for bryophytes. Quadrat 10 (fig. 17), in which both shrub and bryophyte diversity are high, has many young understory trees. It is in a relatively immature open deciduous forest, with many species of bryophyte growing in exposed places on both soil and rock. It seems unlikely that bryophyte diversity can affect that of shrubs and understory trees, but that the reverse is true is only suggested, not proven, by a significant negative correlation.

Is Seasonal Diversity a Factor?

Seasonal diversity is of interest largely in respect to the ground flora stratum of the plant communities studied. There is virtually no seasonal diversity of bryophytes in these Adirondack forests, since bryophytic ephemerals do not occur in these habitats. Nor is there appreciable seasonal diversity on woody plant strata, although some tree seedlings do not appear until summer and many die out in the winter. Seasonal diversity is, however, a noticeable aspect of the herbaceous ground flora. Bulbous or rhizomatous perennials tend to show high productivity early in the season and to die back later, often using light resources available in early spring, but less available under an expanded leaf canopy. This phenomenon increases the total annual diversity of deciduous forests. Several deciduous forests quadrats on Ampersand and Whiteface were surveyed in late summer and again in May to determine the extent of seasonal diversity. Six species were found in the spring survey that had not been found in the same quadrats previously, notably *Erythronium americana*, *Smilacina racemosa*, and *Trillium undulatum*, all spring-flowering perennial herbs with food storage organs. The quadrat in which most additional species were found, quadrat 3 on Whiteface at 1600 ft (370 m), is compared below for late summer (3) and the following spring (3')



(photo by N. C. Slack)

Oxalis montana and *Pleurozium schreberi*, probable competing species on forest floor under *Abies balsamea*.

Quadrat	S	H'
3	14	1.6
3'	20	1.4

There is an increase in species richness from 14 to 20, but very little change in diversity (H'). The Shannon function continues to increase indefinitely as new species are added, but at a diminishing rate. Thus, if one species with a relative abundance of 5 percent were replaced by five equally abundant species, the increase in H' would be only 0.08. If the additional species are not equally abundant, the function may even decrease, as in the present case. The Shannon function may thus undervalue seasonal diversity, but in this forest ecosystem neither the species richness nor the productivity of spring ephemerals is very great compared to that of the plant community as a whole. A much greater contribution in both respects is made by ephemeral vascular plants in other ecosystems, for example, desert summer ephemeral (Whittaker, 1965).



(photo by A. B. Welborn)

Hemlock-hardwood forest on Ampersand Mountain, containing sugar maple, yellow birch, American beech and hemlock.

Study of Epiphytic Bryophytes (Ampersand)

One possible objection to the Adirondack study is that all bryophyte habitats have not been adequately sampled. None of the quadrats was chosen for its "good" bryophyte habitats; the only predetermined factor in the choice of locations was altitude. Since the main object of this study was to measure diversity, areas in which bryophytes were known to be particularly diverse could not be purposely chosen. Nevertheless, certain "good" bryophyte habitats, such as streambanks and wet rock ledges, have been under-sampled by these methods. Many species of bryophytes of specialized microhabitats, found elsewhere in the Adirondacks, have not appeared in any of the quadrats. Detailed studies of communities in such habitats would complement the present study. A valuable quantitative study of one such community, that of rotten logs, has recently been completed by Mühle and LeBlanc (1975). In addition to the quadrat studies, I have made a pilot study of epiphytic bryophyte communities, to determine whether this specialized habitat adds significantly to bryophyte diversity in the Adirondack forest.

Epiphytes on northern hardwood trees are characteristic of undisturbed Adirondack areas with high rainfall. Such epiphytes occur on both Whiteface and Ampersand Mountains, but are relatively uncommon except at the lower elevations on Ampersand (1600 to 2000 ft). True epiphytes on tree trunks were not included in the quadrat studies; tree base communities



(photo by A. B. Welborn)

Epiphytes of *Acer saccharum* on Ampersand Mountain, including *Neckera pennata* and *Porella platyphylloidea*.

were measured up to three decimeters from ground level; but these are quite different from true epiphyte communities further up the trunk.

Epiphytic bryophytes are present largely on four species of trees on Ampersand: *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, and *Tsuga canadensis* (sugar maple, yellow birch, beech, and hemlock). Ten trees of each species were sampled, the only criterion being the presence of epiphytes up to at least two meters. In many cases they were present to 10 m.

I attempted to record all species present, by using a ladder and long pole to reach the upper trunks. As in all parts of this study, specimens which could not be identified with certainty in the field (e.g., species of *Frullania* and *Brachythecium*) were brought back to the laboratory for further study. Diameter at breast height (dbh) was measured for all trees studied. Each tree was treated as a "quadrat" in the analyses of species composition. The results, which follow, have proven interesting even with this limited amount of data.

Nine species of bryophytes were found growing as epiphytes and not found elsewhere in the quadrats on either Ampersand or Whiteface, indicating that this habitat is indeed an additional source of diversity. Furthermore, three other epiphytic species had been found only once before, on a tree base on Ampersand at 1600 ft (490 m). Although tree base communities contain a mixture of true epiphytes and others that are primarily terrestrial, these three species did not occur elsewhere on the ground. Thus I found a total of twelve species growing only as epiphytes.

Different species of trees offer different microhabitats for bryophytes in terms of bark porosity, roughness, exfoliation, chemistry, pH, etc. (Billings and Drew, 1938; Barkman, 1958; Slack, 1976). The effects of such differences among the four species of host trees or phorophytes were examined in terms of species richness (S) of the bryophytes growing on them. The results are as follows:

	Species richness (S)	Max. no. species/tree
<i>Betula alleghaniensis</i>	23	11
<i>Fagus grandifolia</i>	20	10
<i>Tsuga canadensis</i>	7	5
<i>Acer saccharum</i>	23	13

I found a total of 36 species of epiphytic bryophytes, 26 mosses, and 10 liverworts. Many additional species occurred in humus on the tree bases, but these are not true epiphytes and were not included. For comparison, Brown (1948), in a study of epiphytes throughout New York State, found 35 mosses and 19 liverworts growing as epiphytes as defined above. (She found eight additional mosses and six additional liverworts on stumps or tree bases.) Brown's study included 25 stations at elevations from sea level to 5000 ft (1525 m). Seventy-four percent of the moss epiphytes and 53 percent of the liverworts found by Brown, on 63 tree species and over an elevation gradient of 5000 ft throughout the State, were present on only four tree species over an elevation gradient of 5000 ft throughout the State, were present on only four tree species over an elevation gradient of only 400 feet on Ampersand Mountain. Comparisons of my data with those of Brown (1948) and of Phillips (1951) in Michigan are shown in table 5. The bryophytic epiphytes found in the Ampersand study are shown in table 6. Phillips found 38 species of epiphytic bryophytes on 25 different host trees over all of Michigan, including 22 species on the four trees used in the present study. Brown found 38 species on these same four trees, only two more than on Ampersand, although Brown observed trees at more than twenty different sites in the State.

A great many studies have been made of epiphytic bryophytes in North American temperate forests in addition to those of Brown and Phillips. Examples include those of Beals (1965), Billings and Drew (1938), Cain and Sharp (1938), Coleman, Muenscher, and Charles (1956), Culberson (1955), Hale (1955), Hoffman (1971), LeBlanc (1961), and Quarterman (1949). Barkman, who has made extensive studies in Europe, has reviewed the American as well as the European epiphyte literature (1958). I have reviewed much of the subsequent epiphyte literature (Slack, 1976). Many of the earlier studies are concerned with

the classification of epiphyte communities by phytosociological methods. Hoffman studied diversity of epiphytes but on only one host tree, Douglas fir. Beals, Culberson, and Hale considered diversity of epiphytes on a variety of trees in Wisconsin, but, although both tree and epiphyte species overlap with those on Ampersand, the overlap is insufficient to justify extensive comparisons with my data. The number of species and the cover of bryophytes may vary with the age of the tree for any one species, as Quarterman, (1949) showed for red cedar. However, diameter at breast height is a reasonably good indicator of relative age for any one species of tree within a single locality and was used in this study. The relationship between tree size and the number of bryophyte species it supports varies with the species of tree. A linear relationship was not found for any of the four species, but such a relationship was suggested for beech (shown in comparison with sugar maple in figure 18) and might be significant with a larger sample and larger maximum size of trees. I have seen larger beeches and larger yellow birches elsewhere in the Adirondacks, each of which supported a larger number of epiphyte species than the Ampersand trees.



Acer saccharum, showing large population of epiphytic moss, *Neckera pennata* on lower trunk.

(photo by N. C. Slack)

TABLE 5

Epiphytes Compared for Ampersand (present study),
New York State (Brown, 1949), and Michigan (Phillips, 1955)

	<i>Acer.sac.</i>			<i>Fagus grand.</i>			<i>Betula alleg.</i>			<i>Tsuga can.</i>		
	Mich.	NY	Amp.	Mich.	NY	Amp.	Mich.	NY	Amp.	Mich.	NY	Amp.
Mosses												
<i>Amblystegium serpens</i>			x					x				
<i>Anomodon attenuatus</i>	x	x	x		x	x		x			x	
<i>A. minor</i>	x			x								
<i>A. rostratus</i>		x			x						x	
<i>A. rugellii</i>		x	x		x							
<i>Brachythecium oxycladon</i>		x	x		x	x		x			x	
<i>B. salebrosum</i>			x			x			x			
<i>B. starkei</i>		x			x			x				
<i>Brotherella recurvans</i>						x		x	x			x
<i>Dicranum flagellare</i>		x			x			x			x	
<i>D. fuscescens</i>		x			x			x				
<i>D. montanum</i>	x				x	x		x	x	x	x	x
<i>D. viride</i>	x	x			x	x		x	x	x	x	x
<i>Drepanocladus uncinatus</i>	x							x				
<i>Haplohymenium triste</i>	x											
<i>Heterophyllum haldanianum</i>		x			x			x	x			
<i>Herzogiella striatella</i>		x			x			x				
<i>Homomallium adnatum</i>	x				x			x			x	
<i>Hylocomium splendens</i>			x									x
<i>Hypnum pallescens (H. reptile)</i>		x			x	x		x		x	x	x
<i>H. cupressiforme</i>								x				
<i>H. imponens</i>		x			x				x		x	
<i>Leskeella nervosa</i>	x											
<i>Leucodon sciuroides</i>	x		x		x			x			x	
<i>Mnium affine</i>			x			x				x		
<i>Mnium punctatum</i>			x			x						
<i>Neckera pennata</i>	x	x	x		x	x		x	x		x	
<i>Orthotrichum elegans</i>	x							x				
<i>O. obtusifolium</i>	x				x			x			x	
<i>O. pumilum</i>	x				x							
<i>O. sordidum</i>	x				x			x			x	
<i>O. strangulatum</i>									x			
<i>Paraleucobryum longifolium</i>					x			x	x			
<i>Plagiothecium denticulatum</i>		x			x			x			x	
<i>P. laetum</i>			x			x			x			
<i>Platygyrium repens</i>		x	x		x	x		x	x		x	
<i>Pylaisiella intricata</i>		x	x			x						
<i>P. selwynii</i>	x	x	x		x			x			x	x
<i>Rauiella scita</i>		x										
<i>Thuidium delicatulum</i>			x		x	x		x	x		x	
<i>T. recognitum</i>												
<i>Ulota crispa</i>	x	x	x		x	x	x	x	x	x	x	
<i>U. ludwigii</i>					x							
Liverworts												
<i>Bazzania trilobata</i>								x	x		x	x
<i>Cololejeunea biddlecomiae</i>		x						x				
<i>Frullania asagrayana</i>			x			x		x	x		x	x
<i>F. bolanderi</i>	x				x			x			x	
<i>F. eboracensis</i>	x	x	x		x	x	x	x	x	x	x	x
<i>F. inflata</i>						x			x			
<i>Jamesoniella autumnalis</i>					x	x		x	x			
<i>Lophocolea heterophylla</i>		x			x			x	x		x	
<i>Lophozia ventricosa</i>								x				
<i>Plagiochila asplenioides</i>			x									
<i>Porella platyphylloidea</i>	x	x	x		x	x	x	x	x		x	x
<i>Ptilidium pulcherrimum</i>	x	x			x	x		x	x	x	x	x
<i>Radula complanata</i>	x	x	x		x	x	x	x	x		x	x

TABLE 6
Bryophytic Epiphytes, Ampersand Mountain

	<i>Acer.sac.</i>	<i>Fagus grand.</i>	<i>Betula alleg.</i>	<i>Tsuga can.</i>
Mosses				
<i>Amblystegium serpens</i>	x			
<i>Anomodon attenuatus</i>	x	x		
<i>A. rugellii</i>	x			
<i>Brachythecium oxycladon</i>	x	x		
<i>B. salebrosum</i>	x	x	x	
<i>Brotherella recurvans</i>		x	x	x
<i>Callicladium haldanianum</i>			x	
<i>Dicranum montanum</i>		x	x	x
<i>D. viride</i>		x	x	
<i>Homalia trichomanoides</i>	x			
<i>Hylocomium splendens</i>	x			
<i>Hypnum imponens</i>			x	
<i>H. pallescens</i>		x	x	x
<i>Leucodon brachypus</i>	x	x		
<i>Mnium ciliare</i>	x	x	x	
<i>M. punctatum</i>		x		
<i>Neckera pennata</i>	x	x		
<i>Paraleucobryum longifolium</i>			x	
<i>Plagiothecium laetum</i>	x	x	x	
<i>Platygyrium repens</i>	x	x	x	
<i>Pylaisiella intricata</i>	x	x		
<i>P. selwynii</i>	x			
<i>Rhodobryum roseum</i>	x			
<i>Rhytidiadelphus triquetrus</i>	x			
<i>Thuidium delicatulum</i>	x	x	x	
<i>Ulota crispa</i>	x	x	x	
Liverworts				
<i>Bazzania trilobata</i>			x	x
<i>Frullania asagrayana</i>	x	x	x	x
<i>F. eboracensis</i>	x	x	x	
<i>F. inflata</i>		x	x	
<i>Jamesoniella autumnalis</i>		x	x	
<i>Lophocolea heterophylla</i>			x	
<i>Plagiochila asplenioides</i>	x			
<i>Porella platyphylloidea</i>	x	x		x
<i>Ptilidium pulcherrimum</i>		x	x	x
<i>Radula complanata</i>	x	x		

The fact that 23 different species grow on beech and 20 on yellow birch, even though no individual tree had more than 10 or 11 epiphyte species, respectively, indicates a higher potential diversity for larger, older trees. The bark on both of these trees roughens with age, increasing its water-holding capacity and the ease of attachment for bryophytes. Some bryophytes can

become established on smooth bark, *Frullania* species for example, but most cannot. Trees whose bark remains smooth, such as striped maple, *Acer pensylvanicum*, rarely support epiphytes in the Adirondacks. (In the southern Appalachians, under different climatic conditions which affect the bark, it does support epiphytes). Sugar maple, which has a rough bark even

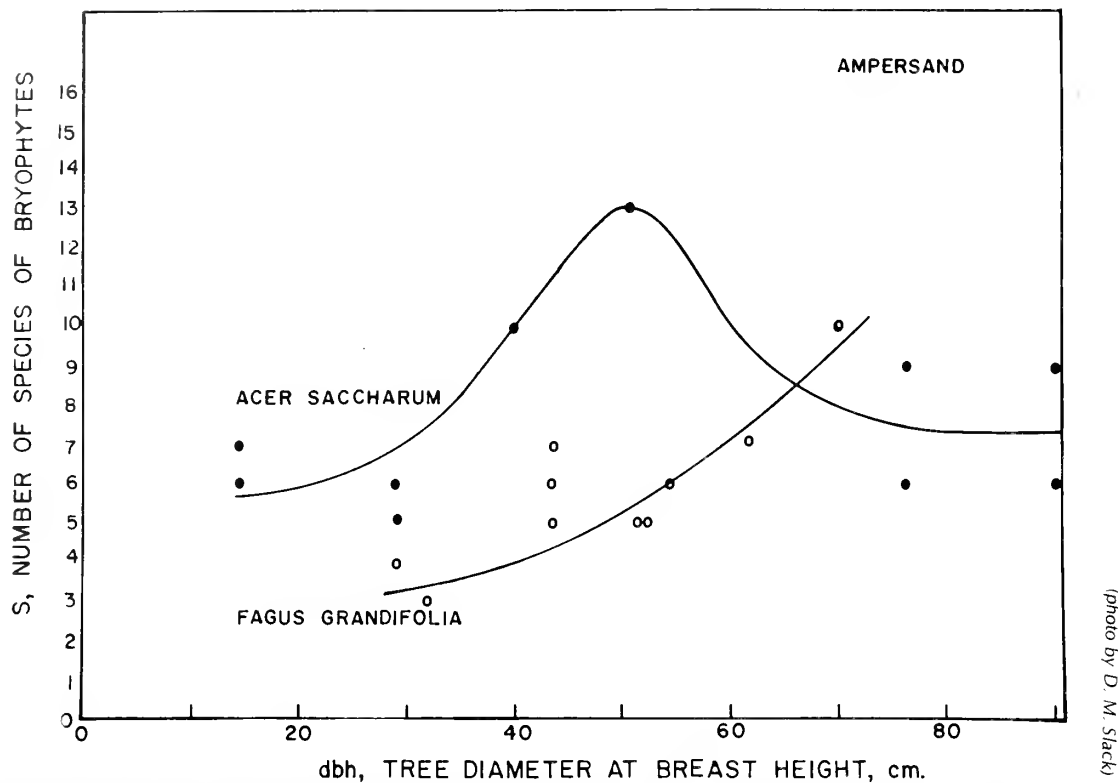


FIGURE 18 Relationship between tree diameter (dbh) and number of bryophytic epiphytes for *Acer saccharum* and *Fagus grandifolia* on Ampersand Mt.



(photo by N. G. Slack)

Epiphytic moss, *Leucodon brachypus*, v. *brachypus*, higher on trunk of *Acer saccharum*.



(photo by N. G. Slack)

Epiphytes on *Fagus grandifolia*, including *Hypnum pallescens* and *Frullania eboraensis*, as well as lichens.

as a young tree, was found to support a large number of epiphytic species even at small dbh.

A succession of species and changes in their relative abundance was found on sugar maple, with *Porella platyphylloidea*, *Neckera pennata*, and *Anomodon attenuata* dominant on different trees, but each of these species, as well as pioneer species such as *Radula complanata*, were found to persist at least in small quantities after their periods of dominance. The present data show an increase in species richness (S) of sugar maple epiphytes up to about 18 in (46 cm) dbh, followed by an increase in dominance and reduction in both S (fig. 18) and H' diversity, but larger numbers of trees and further cover measurements are needed to test this hypothesis. Age-size correlations are not completely reliable even for one locality; trees of one species may grow at different rates because of differences in microtopography, competition, or genetic factors. Increment boring to determine age is currently being used in further studies.

Host specificity of the epiphytic bryophytes on the four trees species was also considered. Using each tree as a separate "plot," I calculated Sørensen indices to compare all 10 trees of one species with respect to species composition of epiphytes. Means for the 45 resulting comparisons for each of the four species were as follows:

<i>Acer saccharum</i>	0.57
<i>Betula alleghaniensis</i>	0.58
<i>Fagus grandifolia</i>	0.48
<i>Tsuga canadensis</i>	0.42

These are high values, especially for sugar maple and yellow birch, showing similar composition of epiphyte communities on any one tree species. Sørensen values between each pair of host tree species were also calculated. Resulting means were as follows:

<i>Acer-Tsuga</i>	0.02
<i>Acer-Fagus</i>	0.13
<i>Acer-Betula</i>	0.15
<i>Fagus-Tsuga</i>	0.27
<i>Fagus-Betula</i>	0.39
<i>Betula-Tsuga</i>	0.41

These values are all lower than those for single species, much lower except for *Fagus-Betula* and *Betula-Tsuga* comparisons, indicating that, while epiphytic bryophytes may not be closely host specific, within any one forest of particular age and climatic conditions, they show preference for particular tree species. Each of these trees presents somewhat different niche opportunities, probably because of differences in bark characteristics. It does appear, however, that bryophytes distinguish poorly between *Fagus* and *Betula* and between *Betula* and *Tsuga*. In the present study, 13 species were present on only one of the four

host trees, eight of these on sugar maple. In addition, four epiphytic species, very characteristic of sugar maple, were found only on that species and on one beech tree, indicating that these and probably most other epiphytes are not strictly host specific, but occur on additional trees of the correct age and stage. All the species found on only one tree species on Ampersand Mountain were also found on other host trees somewhere in New York State in Brown's, (1948) study; in other words, no species was host specific when the whole State was considered.

Some epiphytes switch preferred hosts with relatively small change in latitude, sometimes even where the host tree is present throughout the epiphyte's range. This has been shown in Europe (Barkman, 1958) and in Wisconsin (Hale, 1955). Conversely, the same host tree may bear different epiphytes in different regions. Sugar maple was found to support different "associations" in lower and upper Michigan, *Homallium adnatum* in the former, *Leucodon* and *Neckera* in the latter (Phillips, 1951), climatic differences being important in this study. Many species of epiphytic bryophytes are much more widely distributed than their host trees. For example, many of the species found on American beech (*Fagus grandifolia*) are also present as epiphytes in Europe, but on European beech, *Fagus sylvatica*. But often they also occur on unrelated tree species. Moreover, bryophytes, such as *Neckera*, *Homalia*, and *Leucodon*, which are restricted to or generally occur on trees in tropical and temperate regions, and are found solely as epiphytes in the present study, are epipetric in treeless arctic or alpine regions.

Such switches of substrate are also seen in temperate regions. For example, the liverwort *Frullania asagrayana*, a common Adirondack epiphyte, is found in Minnesota on rock walls. The majority of epiphytes found in the Ampersand study, for example, *Mnium* and *Brachythecium* species, are facultative, not obligate epiphytes. Most of them occur also on rock, soil, or dead wood. Many species occur on both soil and trees, a smaller number on rock and trees, but rarely is a species found on all three substrates. The preferred habitat within one region may be dependent on climate, as noted above. Species epiphytic on beech in the Adirondacks or the Upper Peninsula of Michigan do not occur on beech at Kenrose Preserve (this study) or in lower Michigan (Phillips, 1951). The climate in the two more southern areas is less cool and humid, and the beech trunk habitat correspondingly more xeric. Many of these species do occur at Kenrose and in lower Michigan, but on the ground or on moist logs. A similar change from epiphytic to terrestrial habitats can be seen in Finland (Barkman, 1958).

Few, if any, temperate bryophytes are host-specific in the same sense as fungal parasites of plants. The

host tree, sometimes called a phorophyte to distinguish it from a parasite host, is merely a substrate. The actual bryophyte substrate is usually dead bark tissue. Bryophytes exhibit habitat preference (or degrees of tolerance) in relation to roughness of bark, as well as bark acidity and other chemistry. It appears that relatively few species are tolerant of the tannin in hemlock bark. Roughness of bark is related to water-holding capacity; some epiphytes are found only in fissures or knotholes of the otherwise smooth bark of beech. Some of these variables have been measured (e.g., Hosokawa, et al., 1964; Grubb, et al., 1969), but it is often difficult to interpret factor interactions.

Host tree preferences of closely related species were examined for possible niche separation. More than one species of each of seven genera were present, including two species of *Anomodon*, *Brachythecium*, *Dicranum*, *Mnium*, *Pylaisiella*, and *Hypnum*, as well as three species of *Frullania*. Two species of each of these genera were recorded on one species of tree, indicating that habitat selection in terms of tree species is not all-important for niche separation. (Intragenetic niche separation in terms of substrate certainly occurs in some of these genera. Two closely related species of *Dicranum*, for example, occur in the Ampersand study area, *Dicranum viride* on wood, as an epiphyte and elsewhere, and *D. fulvum* on rock.)

Data for presence (+) or absence (–) of the tree species of *Frullania* on the four host trees are given below:

	<i>Betula</i>	<i>Tsugu</i>	<i>Fagus</i>	<i>Acer</i>
<i>F. asagrayana</i>	+	+	+	+
<i>F. eboracensis</i>	+	–	+	+
<i>F. inflata</i>	+	–	+	–

The fundamental niches (Hutchinson, 1957) of these species probably differ. The fact that *F. asagrayana* was the only species found on hemlock bears out Schuster's (1953) comment that it is the most xerophytic of these *Frullania* species. Niche overlap does, however, appear to be present at least in terms of tree species, and I could discover no habitat preference on the tree itself, for example, north vs. south side, for any of the species. A fourth species, *F. bolanderi*, present in New York but not found in this study, occurs on all four of these trees in Michigan (Phillips, 1951). On the other hand, on only three occasions were two of the *Frullania* species found on the same individual tree. It appears that these sympatric, congeneric species do not have well separated niches; I think they are opportunistic species kept apart largely by stochastic factors. The role of bryophytes as opportunists is discussed below.

It should be noted that epiphytic bryophytes occur on other tree species as well as the four studied on Ampersand and Whiteface Mountains. At lower eleva-

tions, these included *Fraxinus americanus*, *Quercus borealis*, *Ostrya virginiana*, and *Acer rubrum*. At higher elevations, epiphytes were found on *Picea rubens*, *Abies balsamea*, *Pyrus melanocarpa*, and *Betula papyrifera* v. *cordifolia*. Trees of the same genus do not necessarily have similar epiphyte floras; those of *Betula alleghaniensis* and *B. papyrifera* and of *Acer rubrum* and *A. saccharum* are not similar. *Ostrya virginiana*, on the other hand, has a similar epiphyte flora to that of *Acer saccharum*. Bark characteristics are more important than genetic relationships except where these result in similar bark chemistry, as is probably true in the black oak group. All the bryophyte species found as epiphytes on the trees at higher elevations on Ampersand (i.e., spruce-fir zone), as well as all those found by Brown (1948) at four other Adirondack stations, were found also in nonepiphytic habitats in this zone. The epiphytic habitat thus does not increase the bryophyte diversity in terms of species richness at higher elevations on these mountains. That it adds significantly to species richness at lower elevations in the Adirondacks is shown by the present study on Ampersand Mountain.

Contrary to general European (Barkman, 1958), Japanese (Iwatsuki, 1960) and even some recent American (Hoffman and Kazmierski, 1969) practice, no attempt has been made to classify epiphyte communities (or associations, unions, etc.) on the trees on Ampersand Mountain. Although groups of species characteristic of particular trees, especially of sugar maple and hemlock, do occur, the particular combination of species varied with height and aspect even on a single tree, and on any one species of tree with size and location. Dynamic relationships appeared more obvious than fixed associations of species. In many places a bryophyte species, though still recognizable, was dead and had been overgrown by another species. Quarterman (1949) has studied bryophyte succession on red cedar bark, particularly in terms of changing dominants. She aged the trees by increment boring and, although she studied only nine trees, her demonstration of "dynamic behavior of bryophyte species" is impressive. I think this is a good approach to understanding relationships among epiphyte species. Doignon, as reported in Barkman (1958) studied actual succession in time on a single tree over a 30-year period. This is perhaps the ideal method, but in the modern era of pollution and publish-or-perish policies, it seems unlikely that either the epiphytes or the ecologists would survive that long.

New ecological techniques have been applied recently to epiphyte-host systems (see Slack, 1976, for a review). Beals (1965), for example, used ordination methods in the study of corticolous bryophytes and lichens. With such methods, it is possible to sort out the importance of the host tree as substrate as com-

pared to the age or location of the tree. Gradient analysis can also be used with time as the gradient and measured changes in the importance of individual species, species groupings, total biomass and diversity. This can be done with individual trees, trees of one species in one location but of different ages. In the Southern Blue Ridge in North Carolina, I have observed and measured such changes on different aged trunks of the same sugar maple (Slack, 1976). If changes in microhabitat, such as water-holding capacity of bark, could also be measured in relation to time, this would constitute direct gradient analysis.

Another approach to epiphytic vegetation would be to treat trees as islands and to apply principles of island biogeography (MacArthur and Wilson, 1967). Invasion and extinction rates of epiphyte species could be measured and the influence of nearby "islands" determined. Although there has been much discussion of possible long-distance dispersal of bryophytes in relation to their strange geographical distributions (e.g., Crum, 1972), there is little information about their short-range dispersal. It would be interesting to determine whether adjacent trees of the same species and similar size have more similar species composition than those further apart. In the present study, adjacent trees of the same species were eliminated from the sample to avoid this possible factor, but it has not been measured as far as I can discover. In these Adirondack forests, this factor could be tested by using trees that are regularly present but uncommon and have distinctive epiphyte floras. Examples would be hop hornbeam, *Ostrya virginiana* and white cedar, *Thuja occidentalis*, both of which are present together with the major species of the Ampersand study in a forest in the Adirondack Mountain Preserve near St. Huberts, N.Y., where I am currently investigating epiphytes.

Another interesting question in regard to host-epiphyte "island" systems is whether chance "invaders," those species such as *Hypnum imponens*, and *Mnium ciliare* or *M. punctatum*, which are not primarily found as epiphytes, persist for any length of time on these tree "islands" in competition with more usual epiphyte species. An even more intriguing question, which must have been asked by all earlier pursuers of epiphytes and is mentioned by a few, is why are there so many "empty islands?" A tree of the same species and of similar size may grow next to one covered with epiphytes and yet be completely barren of them itself, for no apparent reason. In addition to that source of "empty islands," each new young tree as it grows, like a new oceanic island produced by volcanic activity, represents a new target for invasion. Thus, a continuous supply of open niches for epiphytes exists even in a mature or climax forest.

The relationship between productivity and diversity,

one of considerable current interest (Whittaker, 1967; Loucks, 1970; Auclair and Goff, 1971; Goodman, 1975), can also be considered in regard to epiphytic systems. Whether high diversity, even for trees, can generally be related to high productivity, as Loucks contended, has been questioned by others (Whittaker, 1965; Auclair and Goff, 1969). I have herein questioned this relationship for bryophytes generally; higher diversity did not necessarily accompany the much higher bryophyte productivity found in the spruce-fir forest as compared to the deciduous forest. The same appears to be true in terms of epiphyte productivity and diversity. From my own experience in the Pacific Northwest and from studies in Oregon (Pike, et al, 1975) and in the Olympic Peninsula, (Hoffman, 1971), where extensive mats of epiphytic bryophytes are present, diversity of epiphytes is no greater than in the Adirondacks. The diversity of epiphytes on Ampersand seems high in view of the much lower productivity of epiphytic bryophytes there than in the Northwest. This question needs further quantitative investigation, especially of trees other than *Pseudotsuga menziesii*, on which most of the western studies have been conducted. I have found both higher productivity and higher species richness of epiphytes in the Southern Blue Ridge than in the Adirondacks, but this probably is a result of historical as well as climatic factors (see Anderson and Zander, 1973, and Slack, 1976).

Although much is to be learned from further quantitative studies of epiphytes and from the measurement of ecological factors affecting them, some of these factors can only be distinguished experimentally. Transplant experiments of the sort that Brodo (1961, 1968) has done with lichen epiphytes could be used to study the substrate factor vs. other factors, such as location on the tree or in the forest. Barkman (1958) suggested other methods of experimental manipulation, such as putting up a baffle to prevent water movement down the trunk, or removing certain species to determine the effects of competition. Trees could be thinned to change the light intensity; some balance between sufficient light for photosynthesis and the detrimental effects of heat and exposure in increasing transpiration rate appear to be important. Climatic factors are of primary importance since epiphytes generally occur in areas of high rainfall and low evapo-transpiration rates, but great differences also exist within a single forest. Manmade factors, which also affect epiphyte growth on the tree species studied here, include nutrient-rich roadside dust, probably a partially unrecognized factor in epiphyte studies, and toxic substances near cities or factories, a human disturbance much studied particularly in relation to lichens but also to bryophytes (e.g., LeBlanc, 1961, LeBlanc and Sloover, 1970, and Nash, 1972, for Eastern North American trees). Whether the

investigator uses disturbances created by others, as with pollution effects, or creates his or her own less drastic perturbations, much can be learned from such studies. It seems to me that the living tree with its epiphytes is an easier system to disturb, and thus to study experimentally, than most other aspects of plant communities.

In conclusion, the present study presents well-replicated data on diversity, in terms of species richness, for the four dominant trees of the hemlock-hardwood forest of northern New York. Many suggestions for further research are given. Additional quantitative data, the techniques of gradient analysis and of island biogeography would make possible the study of dynamic relationships of epiphytes. Lichens should be included in future epiphyte studies; competitive relationships between bryophytes and lichens are obvious to an ecologist looking at epiphytes. The majority of past epiphyte studies, however, have been done by specialists on one taxonomic group such as hepatics or lichens in temperate regions, or orchids in the tropics, rather than by ecologists. The interesting problems that epiphytes present to the ecologist are made difficult by the problems of identifying cryptogams (which are omitted from most investigations of plant community ecology for the same reason). Bryophytes, wrote Crundwell (1970), are "the wrong size." They must be identified by a combination of macroscopic and microscopic characters. If we were the size of cockroaches, he wrote, bryophytes would all look distinctive and would even be known by vernacular names "to the cockroach in the street." The same problems apply to lichens, but these problems are not insuperable, even for noncockroach-sized ecologists. Theoretical ecology would also benefit from the study of epiphyte systems.

Results of the Kenrose Preserve Study

The elevations studied as Kenrose Preserve ranged from 1120 to 1510 ft (335–457 m), thus nearly reaching the lowest elevation on Whiteface and Ampersand Mountains, 1600 ft (488 m). The forests at Kenrose Preserve are of entirely deciduous hemlock-hardwood, except for a small admixture of white pine. Many of the same trees, such as *Acer saccharum*, *Acer rubrum*, *Acer pennsylvanicum*, *Fagus grandifolia* and *Tsuga canadensis* are present as on the lower Adirondack slopes. While ash, (*Fraxinus americanus*) is, however, more common at Kenrose. Also, oak-hickory (*Quercus borealis*, *Carya ovata*) forest is present at Kenrose Preserve, but not on Whiteface or Ampersand.

I wanted to determine whether the limited range of elevation at Kenrose Preserve affected the diversity of bryophytes. Both H' and S are plotted against elevation in figure 19. Elevation is significantly correlated with H' ($r = 0.66$). In general, higher elevations have



(photo by C. J. George)

Mixed deciduous forest, Kenrose Preserve showing open aspect.

greater bryophyte diversity than lower elevations at Kenrose, the major exception being at 1380 ft (420 m), where station 5 shows greater diversity (H') than the highest stations at 1510 ft (457 m). Station 5 also has high species richness (S), but other stations at 1380 ft show considerable variability in both H' and S . Elevation is also significantly correlated with degrees of slope ($r = 0.50$), and is negatively correlated with pH ($r = 0.54$). Thus elevation is here, as elsewhere, a complex variable.

Diversity (H') is plotted against log (percent cover) of all bryophytes in figure 20. The correlation coefficient between H' and percent cover is significant (0.65). There was no consistent relationship between bryophyte cover and diversity (H') for the Adirondack quadrats. For the spruce-fir and arctic-alpine zones, the correlation between cover and diversity was negative. For the deciduous forest it was positive, significantly so on Ampersand ($r = 0.98$ for four quadrats). Further investigation is needed. Diversity (H') appears to be low with low percent cover of bryophytes and high where the bryophyte cover is unusually high, but there is a significant amount of variations in intermediate cover values (figure 20).

Figure 21 shows diversity (H') plotted against $\log_e S$ for Kenrose bryophytes, from which it can be seen that $\log_e S$ is a relatively good predictor of diversity (H'); i.e., an approximately straight line relationship is seen on the graph. (See also multiple regression analysis below.) This means that the evenness component of diversity (J') is relatively constant. The J' values do show less variation than in the Adirondacks; all but three of these values fall between 0.52 and 0.75. Thirty percent of the J' values were under 0.6 and 75 percent under 0.7, with a mean of 0.63, which are low values as compared with those found by other workers for birds (Tramer, 1969) and for higher plants (Pielou, 1966). Adirondack values were mostly low, also. The most extreme low evenness value ($J = .31$) at Kenrose was at a station at the base of an unstable steep bank down which water runs each spring. Only one species of moss, *Fissidens taxifolius*, appears to be well adapted to these conditions and accounts for 87 percent of the bryophyte coverage.

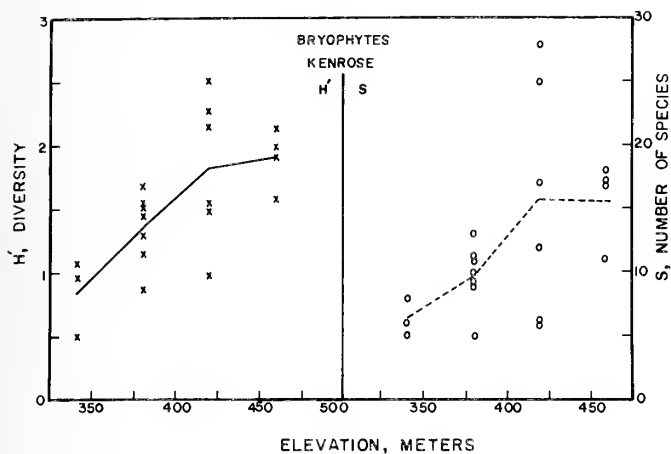


FIGURE 19 Changes in species richness (S) and diversity (H') of bryophytes with elevation change at Kenrose Preserve

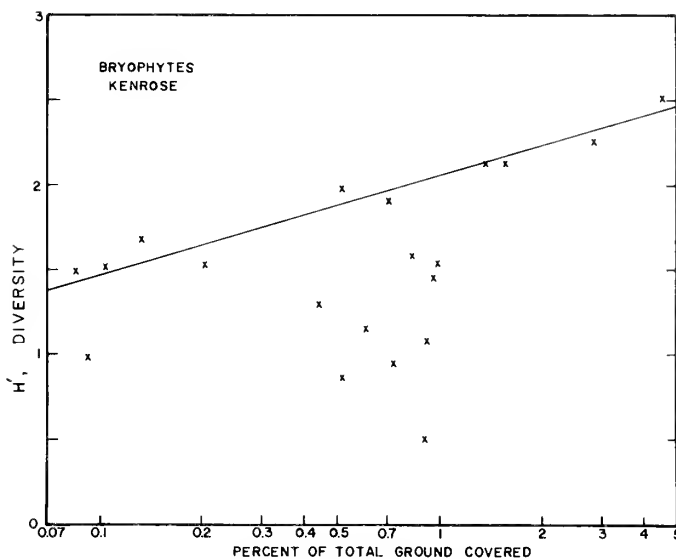


FIGURE 20 Diversity (H') versus log of percent cover of bryophytes at Kenrose Preserve

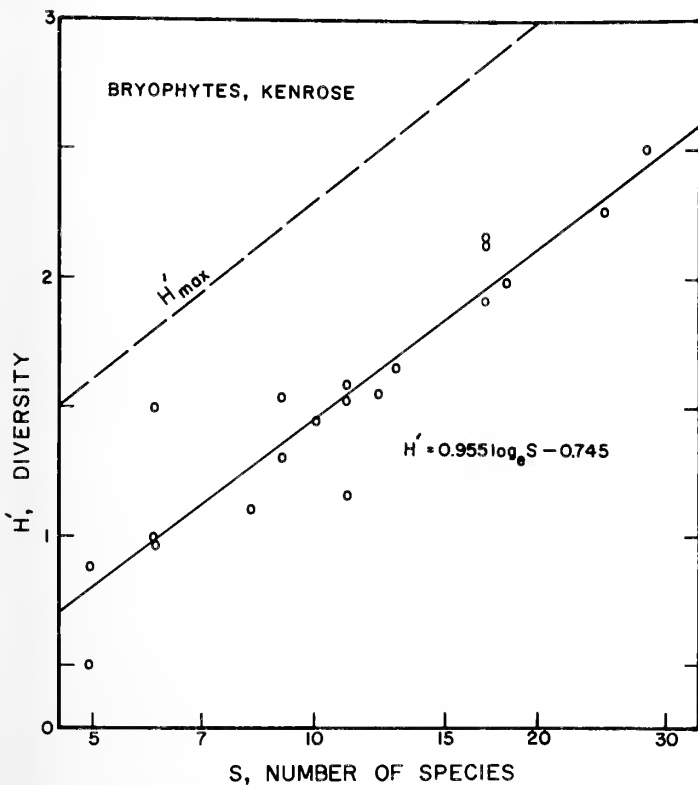


FIGURE 21 Diversity (H') plotted against species richness ($\log_e S$) for bryophytes at Kenrose Preserve

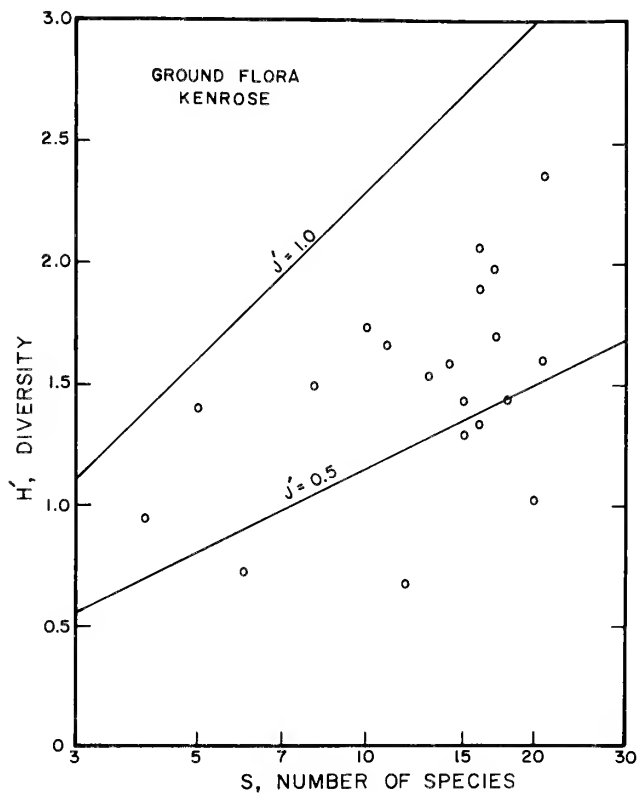


FIGURE 22 Diversity (H') plotted against species richness ($\log_e S$) for ground flora at Kenrose Preserve

Figure 22 shows the relationship between H' and $\log_e S$ for the vascular ground flora at Kenrose Preserve. The majority (65%) of the quadrats have J' values between 0.50 and 0.75, a very similar range to that for bryophytes in almost all quadrats. Low J' values for ground flora, however, do not coincide with low J' values for bryophytes. Dominance relationships for bryophytes are thus independent of dominance relationships for the vascular ground flora. Several vascular plants, for example, are adapted to the unstable bank conditions where *Fissidens taxifolius* was the only important bryophyte.

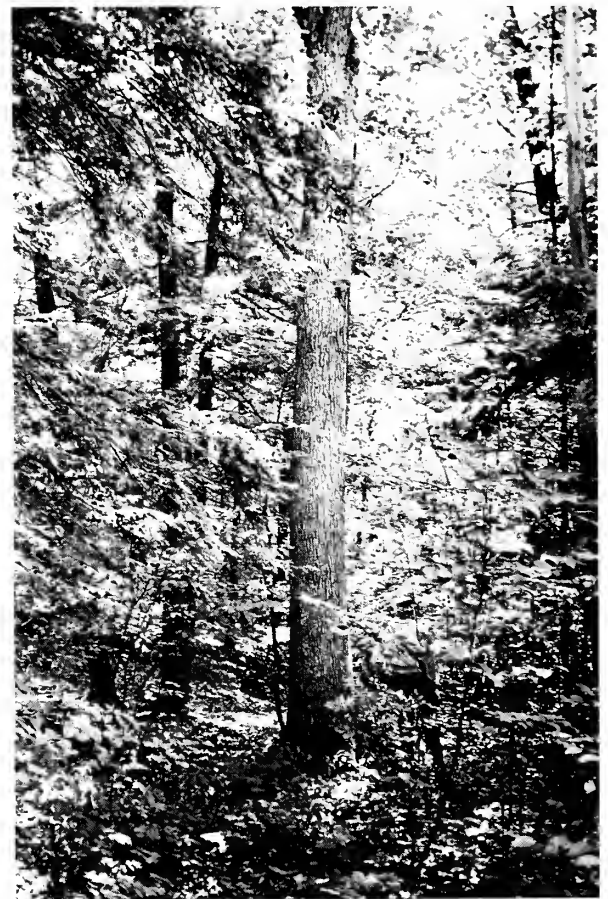
When bryophyte diversity (H') is compared with that for vascular ground flora, an interesting relationship appears. At the higher elevations, bryophytes show higher diversity for almost all quadrats. Below about 1300 ft (400 m), the opposite is true; that is, all the quadrats at 1120 ft (340 m) and the majority at 1250 ft (380 m) show higher diversity of ground flora. It appears from the soil data (see below) that such factors as high calcium and concomitant high pH as well as poor drainage found at the lower elevations may limit bryophyte diversity more than that of vascular plants. Even shrubs show higher diversity than bryophytes in two quadrats at the lowest elevations, 1120 ft (340 m). At all other elevations at Kenrose (fig. 23) and at all stations in the Adirondacks, bryophyte diversity is higher than that of shrubs.

The number of tree species (S) and dominant tree species at the four elevations at Kenrose are seen in figure 24 in relation to bryophyte diversity. The number of tree species per quadrat is correlated with diversity of bryophytes ($r = 0.59$). Highest bryophyte diversity is found in quadrats in which sugar maple is one of the dominants, with several other trees such as hemlock, striped maple, and ash as associates. Diversity is lowest in quadrats in which ash is the sole dominant. High diversity was found also in the oak-hickory forest present on the crest of a hill at 1500 ft (525 m) and above. Although diversity here is not as high ($H' = 1.98$) as in some of the quadrats under sugar maple ($H' = 2.3, 2.5$), seven of the 18 species found in this oak-hickory forest were not found elsewhere in the Kenrose study. Thus, forest type can add to the overall beta diversity for an area whether or not one type of forest has a more diverse bryophyte flora than another. This was found to be true in the Adirondack study areas which encompassed both deciduous and conifer forest, but that it is true even within the deciduous forest biome shown here.

Many environmental factors were measured at Kenrose Preserve. These measurements were made in the same quadrats in which the vegetation was investigated by Carl George and associates. (See Study Area section.) The following variables, which might have some significance for bryophyte diversity, were se-

lected for a multiple regression analysis: elevation, degree of slope, percent of full sun under tree canopy, pH of soil, calcium content of soil, soil temperature, relative humidity, and maximum air temperature. In addition, the following aspects of the vegetation were included in the analysis: total density of bryophytes per 4 by 16 meter quadrat, total density of vascular plants, $\log_e S$ for bryophytes, and number of tree species. Other variables, such as soil type, slope angle, phosphorus and organic content of soil, and minimum summer temperature were eliminated earlier when no correlation with bryophyte diversity was found for any of these factors. Two factors not included may be important. These are drainage, which ranges from poor to good in the study area, and the relative maturity of the forest. Good drainage and later successional stages appeared to favor bryophyte diversity, but neither of these variables had been sufficiently quantified to use in the regression analysis.

Hemlock-hardwood forest, Kenrose Preserve, *Acer saccharum* and *Tsuga canadensis* dominants. Bryophyte diversity was high in forests where sugar maple was dominant.



(photo by C. J. George)

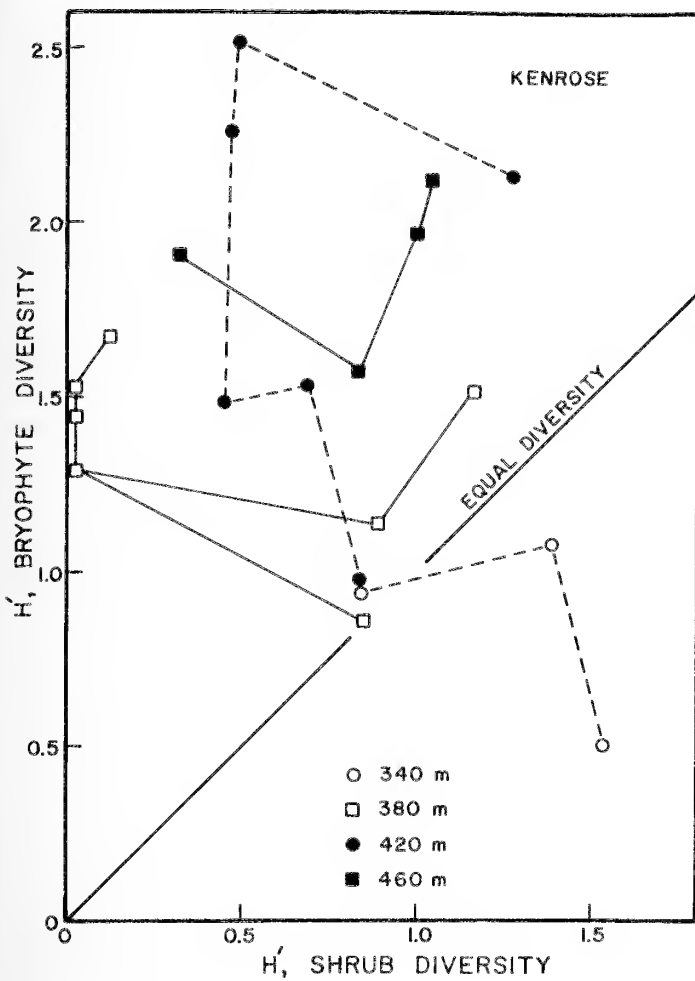
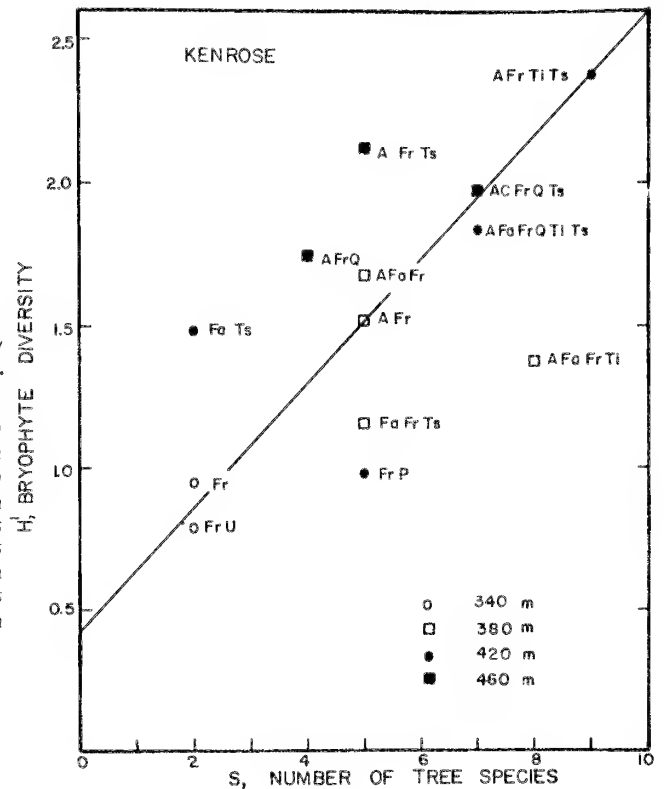


FIGURE 23 Bryophyte diversity (H') plotted against shrub diversity (H') at Kenrose Preserve

FIGURE 24 Number of tree species (S) in relation to bryophyte diversity (H'). Dominant tree species at each of the four elevations are also shown. Key:

A *Acer saccharum*
 C *Carya ovata*
 Fa *Fagus grandifolia*
 Fr *Fraxinus americana*
 P *Pinus strobus*
 Q *Quercus borealis*
 Ti *Tilia americana*
 Ts *Tsuga canadensis*
 U *Ulmus americana*



Regression Analysis

Four separate analyses were made using some or all of the 11 variables, in a stepwise multiple regression analysis program (STEPREG1; SUNYA Code: STAT/02). The results of the regression analyses are shown in table 7. Correlation coefficients between bryophyte diversity (H') and various environmental and other parameters are shown in table 7b. The entire correlation matrix is given in table 8.

The first analysis (1, table 7a utilized $\log_e S$ (or H'_{max}) only. (Recall the evenness component of diversity, $J' = H'/H'_{max}$). As stated above, the evenness component of bryophyte diversity was low but rela-

tively consistent. Therefore, at Kenrose (but not in the two Adirondack study areas), diversity (H') can be predicted reasonably well from the number of species present. The coefficient of determination is 0.87; the regression equation predicts H' from $\log_e S$ as follows:

$$H' = 0.9553 \log_e S - 0.745$$

When all variables except $\log_e S$ are retained in the regression analysis (2, table 7a), only elevation and bryophyte percent cover were significant, although several other variables are significantly correlated with H' . These other variables are not significant in the regression analysis because they themselves are correlated with the significant variables (table 8). For exam-

TABLE 7a
Results of Stepwise Multiple Regression Program for
Environmental Factors and Other Parameters Determining
Bryophyte Diversity (H') at Kenrose Preserve

Type of Analysis	variables	Reg. Coeff.	Std. Error	T	Coeff. Det.
1. $\log_e S (=H'_{max})$	Log S (bryophytes)	0.955	0.087	11.01	0.87
	(cumulative)				
2. Best X (excluding $\log_e S$)	Elevation	0.0021	0.0005	4.25	(0.47)
	Bryophyte cover	0.0000	0.0000	3.13	0.72
	(No. tree species)	0.0535	0.0304	1.76	0.77)
3. Best X (excluding all bryophyte variables)	Elevation	0.0023	0.0006	3.67	(0.47)
	No. tree species	0.0919	0.0342	2.69	0.67
4. Best X (excluding all plant variables)	Elevation	0.0021	0.0007	2.93	(0.47)
	Slope (degrees)	0.0219	0.0111	1.98	0.57

TABLE 7b
Correlation Coefficients Between Bryophyte Diversity (H') and
Environmental and Other Parameters at Kenrose Preserve

Significant correlation coefficients with H'

$\log_e S (=H'_{max})$	0.93
Percent cover, bryophytes	0.63
Number of tree species	0.58
Degree of slope	0.59
pH of soil	-0.45

Nonsignificant correlation coefficients with H'

Percent cover, vasc. plants	0.037
Percent of full sun	-0.14
Calcium (kg/hectare)	-0.36
Soil temperature	0.087
Maximum air temperature	0.099
Relative humidity	0.072

ple, the number of tree species (table 7b) would raise the coefficient of determination to 0.77 but is not quite significant in the present analysis (2) because of its correlation with bryophyte cover (Denbry, table 8).

The third equation used (3, table 7a) excluded all bryophyte variables including bryophyte cover. Here elevation and number of tree species had significant regression coefficients and together account for 67 percent of the variation in H'.

Finally, a fourth analysis (4, table 7a) utilized an equation excluding all the plant variables, using only nonbiotic factors. Here elevation and the degrees of slope, the latter being only marginally significant, accounted for 57 percent of the variation in H'. Although elevation alone accounts for almost half of the variation in bryophyte diversity (H'), biotic factors are also important variables, and together with elevation account for about 75 percent of the variation found.

It should be noted that pH has a significant negative correlation ($r = 0.45$) with H' but does not have a significant regression coefficient in any of these analyses. This is explained by the fact that soil pH also has a significant negative correlation with slope ($r = -0.79$) and with elevation ($r = -0.47$), both of which were used in all analyses. Brophyte diversity in this study is low where the pH is high (pH 6 or above), and these quadrats are in areas of both low elevation and low slope at Kenrose. The pH of the soil was found to be correlated with Kg/hectare of calcium in the soil ($r = 0.88$), high pH resulting from high calcium. The correlation between calcium and diversity is not quite significant ($r = -0.36$); very high calcium is associated with low diversity, but so is very low calcium. Intermediate ranges of calcium have little relationship to diversity. The relationships between soil ealcium, ele-

vation, and bryophyte diversity (H') can be seen in figure 25. I interpret these data to indicate that the tolerance range for bryophytes both in terms of biomass (measured as total percent cover) and of diversity (H') is limited by low and very high calcium. In the intermediate range for soil calcium, presumably optimal for most forest bryophytes, diversity and biomass are limited by other factors such as humidity, or more likely by an interaction of such factors.

Elevation, even over the short range found at Kenrose Preserve, is a complex variable involving slope angle, soil chemistry, and probably soil drainage as well. Even more complex interactions are indicated. Slope angle, for example, was found to influence temperature, incident light, and relative humidity, none of which, when examined separately, was found to be a significant determinant of diversity. Such interactions cannot always be sorted out by multiple regression analysis techniques. Ultimately, experimentation is needed.

Perhaps the most striking result of the study of microclimatic variables at Kenrose was that so few of them were significantly correlated with diversity. Two conclusions can be drawn from this result: first, some variables such as summer soil and air temperatures are probably not relevant to bryophyte growth or diversity over the small range of these factors within the study area. The same factors might be important in a similar-sized or smaller area in which the microclimates are more severe, such as the summit of Whiteface Mountain. Important studies correlating microclimate and plant growth, such as those of Bliss (1969), have been made in areas with sharp microclimatic gradients.

TABLE 8
Correlation Matrix for Environmental and Other Parameters at Kenrose Preserve

H' _{max}	Denbry	Denvasc.	Trees	Slope	Elev.	%Sun	pH	Ca.	Soil temp.	Rel. hum.	Max. temp.	H'
.64	.043	.65	.53	.59	-.15	-.36	-.24	.023	.025	.033	.93	H' _{max}
	.26	.44	.44	.11	-.19	-.22	-.059	-.21	.27	.057	.63	Denbry
		-.24	-.14	-.11	.50	.52	.55	-.010	.015	.090	.037	Denvasc.
			.44	.31	-.32	-.44	-.41	-.16	.19	-.15	.58	Trees
				.46	-.26	-.79	-.60	.16	-.067	.11	.60	Slope
					-.18	-.47	-.32	.22	-.14	.29	.66	Elev.
						.48	.24	.58	-.57	.23	-.14	%Sun
							.88	-.30	.26	-.19	-.45	pH
								-.45	.51	.012	-.36	Ca.
									-.94	.50	.087	Soil temp.
										-.34	-.072	Rel. hum.
											.099	Max. temp.
												H'

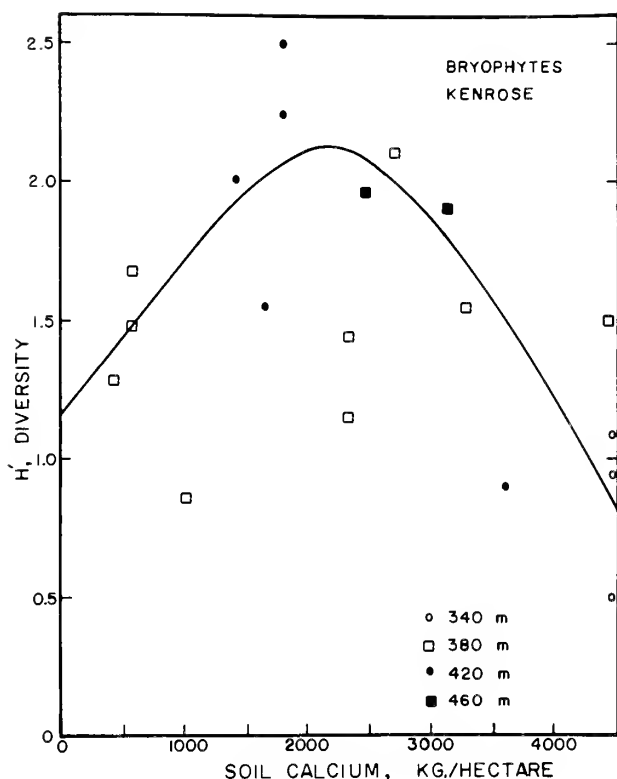


FIGURE 25 The relationship between soil calcium, elevation and bryophyte diversity (H') at Kenrose Preserve



Oak-hickory forest, Kenrose Preserve; seven bryophyte species were found only in this forest type at Kenrose.

Second, microclimatic measurements should be as closely related as possible to the stratum or type of plant under study. Relative humidity and light intensity at two meters above ground level are appropriate to the shrub layer, but may be of little significance for bryophytes growing at two centimeters or less above the soil.

When I reexamined the high diversity quadrats at Kenrose Preserve after the completion of this study, I observed another probable factor affecting bryophyte diversity, the heterogeneity of the quadrat or station in terms of possible bryophyte substrates. Since most bryophytes cannot survive being covered by annual leaf fall, they are restricted in deciduous forest to substrates not covered by leaves. These include rotting logs, tree bases, tree trunks, outcropping rock, boulders, and steeply sloping ground. Such substrate diversity could be measured by the Shannon formula, using percentages of area covered by rock, logs, etc. Poulson and Culver (1969) have used a similar measure in their study of diversity of cave inhabitants (all heterotrophs), but it has not been used to my knowledge in alpha diversity studies of plant communities. Further subdivisions of substrate, for example, into acid and basic rock, decorticated logs and those with bark intact, etc., would also be appropriate in relation to bryophyte diversity. Different species are adapted to particular substrates as Mühle and LeBlanc (1975)

have recently shown for both mosses and hepatics on logs in various stages of decay. This method of study of alpha or within-habitat diversity would also be applicable to quite different communities, for example the attached microflora and fauna of freshwater ponds, where the substrates would be macrophytes, filamentous algae, wood, etc.

Beta or between-habitat diversity was evident at Kenrose Preserve in spite of the small elevation gradient. Cluster analysis (see Slack, 1971) showed that clusters of quadrats at the same station all had significant B-coefficients based on the Sørensen index for species similarity, whereas clusters of quadrats including the highest and lowest elevations have B-coefficients ranging down to zero, that is, zero similarity of species composition within a cluster. Beta diversity is also evident in the species composition of the station in dry oak-hickory forest. In one 4 by 16 quadrat at this station, seven species of mosses were recorded that were not found elsewhere in the Kenrose Preserve study.

Taxonomic Diversity

Table 9 shows the partitioning of bryophyte diversity (H') into components by family, genus, and species. If each species in a quadrat belongs to a different family, 100 percent of the diversity is family di-

versity. This was the case in the low diversity quadrats at Kenrose Preserve. Similarly, if each species belongs to a different genus, 100 percent of the H' diversity is family plus genus diversity. If there are thus no congeneric species, H' is the same whether calculated by species or by genera, as in arctic-alpine quadrat 21 on Whiteface Mountain. (See the last column of table 9 for H' calculated by genera.)

Where H' is high, as in the spruce-fir quadrats at Whiteface and in some of the deciduous forest quadrats at Kenrose Preserve, it can be seen (table 9) that a relatively high percentage of the diversity is at the species level; that is, many belong to the same genera. For these high diversity quadrats ($H' = 2.13$ to 2.63), the percentage of diversity resulting from congeneric species ranged from 10.4 to 16.0 (mean = 13.5). For the two highest diversity quadrats in these two locations (3 at Kenrose and 20 at Whiteface; see table 9) generic diversity was also high, 11.0 and 12.9 percent, respectively. These two quadrats also had high specific diversity (because of congeneric species), indicating that species packing goes on at both the generic and specific levels where there are many species per quad-

rat. Other quadrats in these two groups (table 9) show generally low generic diversity, from 1.9 to 6.3 percent (mean = 3.9). In all of the quadrats discussed above, the familial fraction of diversity is high, from 71 to 86 percent, that is up to 86 percent of the species in a quadrat are members of different families. When I compared these with those of Lloyd Inger, and King (1968), who partitioned diversity of amphibians and reptiles of a Bornean rain forest, I found the familial fraction of diversity in their study much lower, up to 50 percent for frogs and lower for lizards and snakes. These three groups, however, constituted a total of only 15 families, whereas over 40 bryophyte families are represented in the present study. The generic fraction of diversity for both amphibians and reptiles was higher than in my bryophytic study as is the specific fraction for frogs and lizards, but not for snakes. The authors concluded that "only a small part of the total species diversity. . . is attributable to congeneric species living together," but actually that percentage was 20 percent for frogs and 27 percent for lizards; these percentages do not seem to me to be insignificant.

TABLE 9
Taxonomic Diversity—Partitioning of H'
by families, genera and species

Quadrat No.	Total Diversity (H')	% Family	% Genera	% Species	Diversity (H') by Genera
Whiteface Mt.—Spruce-fir quadrats					
16	2.29	78.60	6.32	15.08	1.94
18	2.28	86.07	3.50	10.43	2.04
20	2.63	71.08	12.92	16.00	2.21
Whiteface Mt.—Arctic-alpine quadrats					
21	2.13	82.96	17.04	0.00	2.13
22	1.37	94.53	0.00	5.47	1.30
23	1.54	52.77	21.28	25.95	1.14
24	0.56	25.13	69.38	5.49	0.53
25	1.66	75.07	16.52	8.41	1.52
Kenrose Preserve—Deciduous forest quadrats					
Low diversity quadrats					
8	0.50	100.00	0.00	0.00	0.50
11	0.98	100.00	0.00	0.00	0.98
15	0.95	100.00	0.00	0.00	0.95
17	0.86	100.00	0.00	0.00	0.86
High diversity quadrats					
3	2.51	74.12	10.95	14.93	2.14
4	2.26	85.94	1.93	12.13	1.98
12	2.13	85.33	3.54	11.13	1.90
18	2.14	80.76	4.17	15.07	1.81

Species diversity was also partitioned for two other groups of quadrats: the low diversity quadrats (H' less than 1.0) at Kenrose, and the five arctic-alpine quadrats at Whiteface. In all four of these Kenrose quadrats (table 9) the familial diversity was 100 percent; that is, each of the species belonged to a different family. This result is not surprising since the total number of species for these quadrats ranges only from five to nine; a random selection of species could yield this result. Apparently, species belonging to several different families are adapted to conditions in these quadrats: high soil calcium, high pH, and instability because of spring soil movement. High Percentage Similarity between some of these quadrats, especially the value of 0.77 for quadrats 8 and 15, which are separated from each other, indicates that certain species are indeed specialists for these conditions.

The arctic-alpine quadrats differ greatly from each other when diversity (H') is partitioned into familial, generic, and specific portions. Quadrats 23 and 24 (table 9) have the highest specific diversity (26 percent) and/or generic diversity (69 percent) of any of the quadrats computed, whereas two other quadrats (21 and 22) have 0.0 specific and generic diversity, respectively. Quadrats 21, 22, and 25 show high familial diversity (75 to 95 percent of the species belonging to different families). In 23 and 24, however, only 25 and 53 percent of the diversity is familial. In these quadrats, two families, Grimmiaceae and Polytrichaceae and three genera, *Grimmia*, *Polytrichum*, and *Pogonatum* account for a large percentage of total diversity. A total of seven species is involved. These genera, and particularly their representatives on the summit of Whiteface, have adapted to the high winds and insolation found on the summit by the reduction of transpiration. In these quadrats, the selection of a few species from a large number of families is not random, as it may be in the low diversity quadrats at Kenrose; a much smaller number of families have representatives adapted to these severe arctic-alpine conditions.

Figure 26 shows some general relationship between the number of congeners and the number of species (S) for all Kenrose quadrats; quadrats with large numbers of species tend to have more congeners than those low species richness. The quadrat with highest species richness had 14 congeners, indicating that high species diversities are made possible, at least in part, by species packing and habitat selection in such genera as *Dicranum* (see below). On the other hand, MacArthur (1969) has pointed out that the higher number of bird species within a limited area in the tropics may be largely an increase in genera rather than in congeneric species. He cites an example from Barro Colorado Island, Panama, compared with a

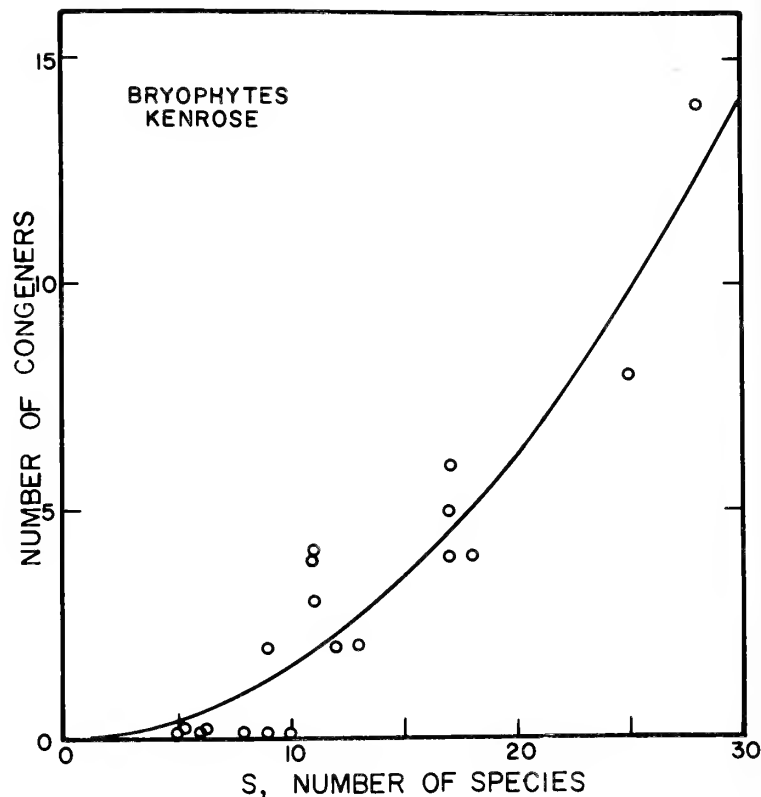


FIGURE 26 Number of congeneric bryophyte species in relation to species richness (S) at Kenrose Preserve

Vermont woodland. Simpson (1964) has pointed out the increase in the number of families of recent mammals in the American tropics as compared with the temperate zone.

There is much evidence, however, that a large percentage of tropical diversity, at least for plants, is at the specific level. Tropical congeners abound both in bryophytes and vascular plants. The liverwort genus, *Plagiochila*, which has only one representative in New York State, is tremendously diverse in the tropics, with several hundred species, many occurring together (Schuster, 1966, S. R. Gradstein, personal communication). Richards (1969) noted that the large number of species of several different vascular genera, *Shorea* and *Miconia*, for example, which occur as congeners in the tropical rain forest in Asia and tropical America, respectively.

My data suggest that the relative number of bryophyte congeners increases in both difficult low diversity habitats and in very favorable high diversity habitats. The large number of congeners in high diversity areas may be a widespread phenomenon in plants and perhaps in some groups of animals also. Wake (1970) notes the remarkable speciation of one tribe of tropical salamanders, the Bolitoglossini of the family Plethodontidae. He attributes this speciation to the availability of numerous types of niche that are suitable for these salamanders in the tropics.

From the analysis of taxonomic diversity, I conclude that the species is the most appropriate level on which to study bryophyte diversity. Questions that are raised concerning taxonomic diversity can also be examined by analyzing habitat preferences of congeneric species occurring in the same quadrat. Johnson and Raven (1970) state that a forest with four different oaks should be considered just as diverse as one with species of four different genera as dominants. I think that at least as good a case can be made for some bryophyte genera in the present study as for oaks. Consider, for example, the moss genus, *Dicranum*, of which at least six relatively common species occurs in the Adirondacks. Three species of *Dicranum* were found as congeners in 70 percent of the spruce-fir and deciduous quadrats at Whiteface and Ampersand Mountains; 25 percent of the quadrats contained four species of *Dicranum*. The various species were found to have distinct habitat preferences which, although not absolute, are at least as well marked as between many species of different genera. For example, *Dicranum fulvum* is found on rock, whereas the morphologically similar *Dicranum viride* is found on wood, sometimes as an epiphyte on tree trunks. *Dicranum montanum* is found in several habitats, but commonly on tree trunks. It is, however,

a more xeric species than *D. viride* and is often found higher up the trunk on the same species of tree, or on more xeric tree species. For example, *D. montanum* was regularly found on *Tsuga*; *D. viride* never was. (This might be due to chemical rather than water-holding differences in the bark, but in either case the two species of *Dicranum* show habitat preferences.)

Dicranum scoparium, although also occurring in rotten wood, was the only one of these species commonly found on the ground. *Dicranum fuscescens* was found on rotting wood, as was *D. flagellare*. Here there was at least a partial separation by elevation, with *D. fuscescens* at higher elevations. *Dicranum flagellare* occurs regularly on very rotten wood. Other species, such as *D. undulatum*, occur largely in boggy areas. In this genus at least, species are indeed ecological equivalents in terms of diversity. It would be possible, although somewhat more difficult, to make a similar case for congeneric species of *Hypnum* and even for most species of *Brachythecium* found in this study, some of which, however, are not congeneric in the same quadrat because of altitude preferences.

In a few genera, habitat preference was not evident among congeneric species. This was true for epiphytic species of *Frullania* on Ampersand Mountain and for arctic-alpine species of *Polytrichum*, *Pogonatum*, and *Grimmia*. These genera, all living under extreme conditions, seem to me to represent a different phenomenon from the above. The species of *Pogonatum* or *Grimmia* living on a treeless mountain summit and the species of *Frullania* living on the smooth, dry bark of a beech, are each similarly adapted to these particular environmental conditions. It seems that a community of three macroscopically similar *Frullania* species is less diverse than a *Neckera*, *Porella*, *Anomodon* community on a neighboring sugar maple, whose bark does not constitute so extreme an environment. The example of four oaks may be more similar to that of the three *Frullania* species than to the *Dicranums*. Several species of oak may live under rather extreme conditions, such as those of drought and recurrent fire in the Albany pine bush (sand plains) area, and have similar adaptations to these conditions. For oaks in this sort of environment and for bryophyte genera of difficult environments, a good case could perhaps be made for studying diversity in terms of genera. The majority of the congeneric species of bryophytes in less extreme habitats in this study, however, showed ecological separation, although not in all genera as distinctly as in *Dicranum*.

Further Aspects of Community Structure

Populations, Communities, and the Elevation Gradient

Elevation has proved to be a very important variable for bryophyte species diversity in this study. The effect of elevation range within a large area, the changes in species composition of bryophytes (and also of vascular plants) over a 1000 m range of elevation in the Adirondacks, and diversity changes even over the 130 m range of elevation at Kenrose Preserve have all been documented in this research. Each plant stratum has been shown to have a different pattern of diversity (H') and of species richness (S) over the elevation gradient studied on the two Adirondack mountains. Numbers of species of mosses and especially of liverworts varied with elevation and with vegetation types resulting from elevation change. In New York State and also in other geographical areas, for example, Glacier National Park, Montana (Herman, 1969) and Costa Rica (Crosby, 1969), species richness of bryophytes is high in areas where the elevation gradient is large.

The type of analysis used in this research, especially that involving the comparison of species composition along the elevation gradients at Whiteface and Amper-sand and at Kenrose Preserve, is generally called direct gradient analysis (Whittaker, 1956, 1968, 1970). In contrast to this type, indirect gradient analysis is used where there are no obvious environmental gradients that can be measured; the latter are inferred from the vegetation samples themselves and their changes in species composition.

Population of single species can also be studied by direct gradient analysis. The term "plant community" has been used throughout this paper in Whittaker's (1967) sense of a "particular, limited area of vegetation which seems homogeneous." The vegetation of any particular quadrat may be considered a sample of the immediately surrounding homogeneous appearing community. These communities do not, however, have sharp boundaries except where a very sharp edaphic or topographic change occurs. Although the composition of these communities changes with elevation (as can be seen in this study from the Sørensen and Percent Similarity indices), this community change is a result of separate density changes for each species along the elevation gradient. The pattern of density change with elevation differs for each species and usually takes the form of a bell-shaped curve for tree species. Whittaker (1968) shows such curves for pines and oaks in the Great Smoky Mountains between 400 and 1400 m.

Similar curves can be drawn for beech, sugar maple, yellow birch, red spruce, and balsam fir from my Adirondack data, with peaks for each species as follows, based on density of individual trees:

<i>Fagus grandifolia</i>	1600 ft (490 m)
<i>Acer saccharum</i>	2000 ft (610 m)
<i>Betula alleghaniensis</i>	2800 ft (850 m)
<i>Picea rubens</i>	2800 ft (850 m)
<i>Abies balsamea</i>	4000 ft (1200 m)

Curves for these species from 53 sites in the Whiteface area (Scott and Holway, 1964) show very similar peaks. Such changes with elevation for each species are not so marked over the much smaller elevation range at Kenrose Preserve, but even here some species, such as elm and ash, have their highest density at the lowest elevation while others, such as red oak and hickory, have highest density at the higher elevations. Some species, sugar maple, for example, are present throughout the elevation range at Kenrose.

When such curves are examined for individual bryophyte species, simple bell-shaped or binomial curves do not always result. The physiological tolerances of some species (c.f. *Andreaea rupestris*, fig. 12), enable them to live over the whole elevation range on Whiteface Mountain. For trees and almost all other vascular plants on Whiteface, the vertical distributions are limited by physiological tolerances, or where tolerances are marginal, by competition with other species better adapted at particular elevations. Sørensen and Percent Similarity values for vascular plants at 1600 ft (488 m) and at 4800 ft (1463 m) are all 0.0; i.e., no vascular plants extend over the entire elevation gradient. For bryophytes, however, the values for these indices, although very low, do not reach 0.0. Such species as *Andreaea rupestris* and *Grimmia apocarpa* occur in both deciduous forest and arctic-alpine vegetation on Whiteface. They are absent, however, where suitable rock substrate is not found; thus, plotting relative density (cover) vs. elevation for such species may result in bimodal or irregular rather than smooth binomial curves.

Figures 27 and 28 show generalized curves, prepared from the relative cover data, for 13 bryophyte species. It can be seen that each species has its own distribution pattern, although these patterns may be similar. Whether we see a continuum, with each species in turn reaching a peak density at a particular elevation, the view of most current American ecological theory, or communities of species with similar physiological tolerances occurring together in a quadrat at a particular elevation, as in most current continental European ecology, depends largely on our point of view. Both points of view are valid and useful, provided that the dynamic aspects of communities are not

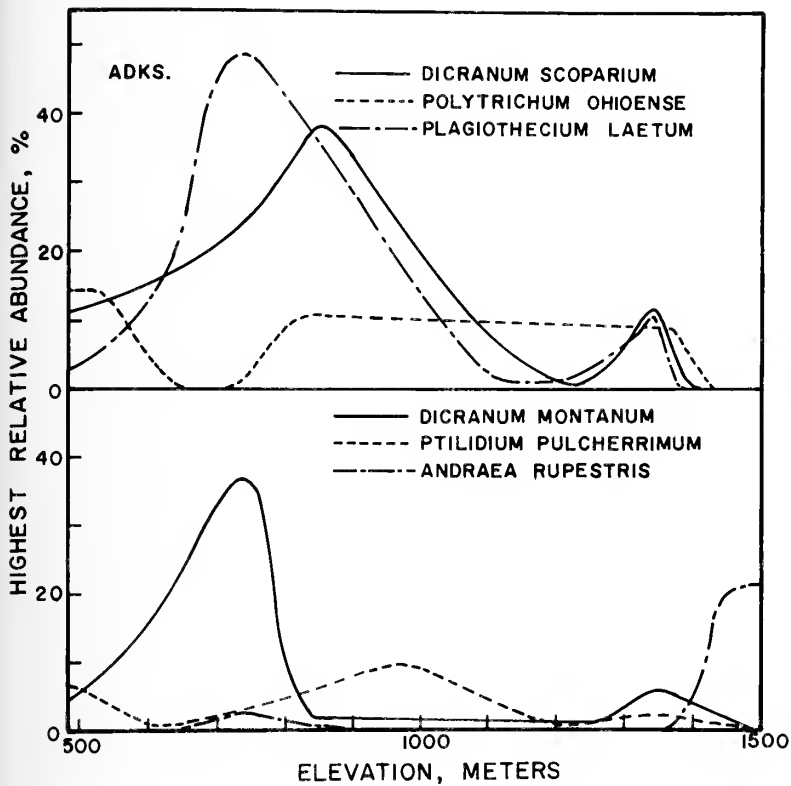
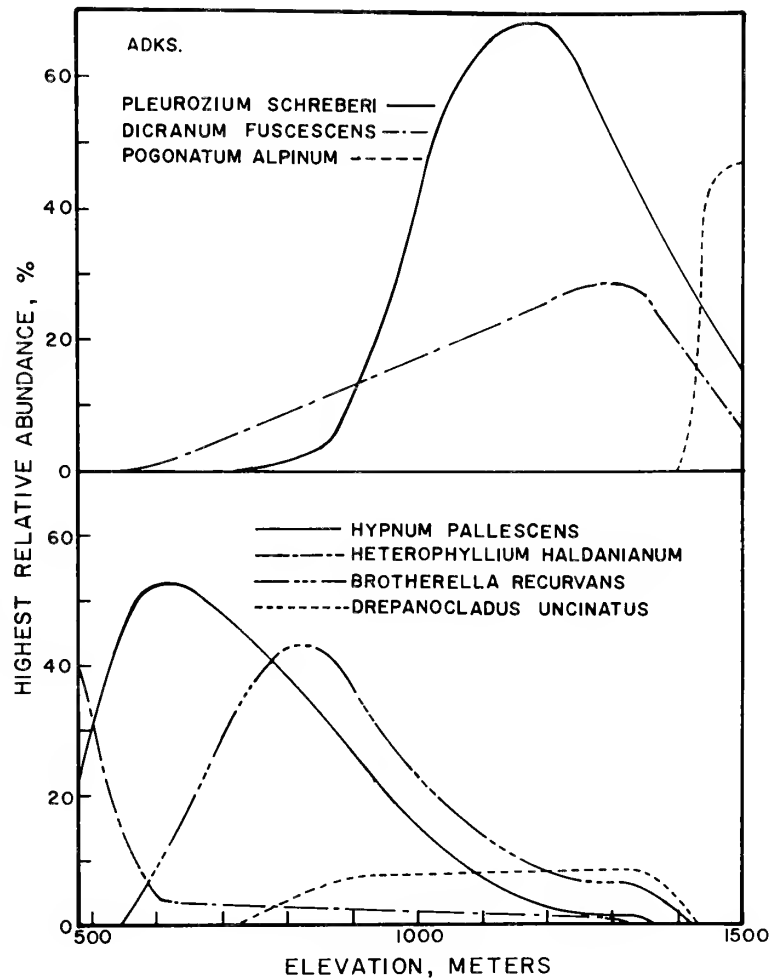


FIGURE 27 Generalized curves for abundance of the following bryophyte species in relation to elevation on Whiteface and Ampersand Mts.

Andreaea rupestris
Dicranum montanum
Dicranum scoparium
Plagiothecium laetum
Polytrichum ohioense
Ptilidium pulcherrimum

FIGURE 28 Generalized curves for abundance of the following bryophyte species in relation to elevation on Whiteface and Ampersand Mts.

Brotherella recurvans
Dicranum fuscescens
Drepanocladus uncinatus
Heterophyllum haldanianum
Hypnum pallescens
Pleurozium schereberi
Pogonatum alpinum





(photo by A. B. Wellborn)

Flag trees (*Abies balsamea*) below timberline, Whiteface Mountain, showing importance of prevailing wind direction.



(photo by D. M. Slack)

Whiteface Mountain in late December showing snow cover, spruce-fir and arctic-alpine zones.

obscured by overzealous classification. Phytosociological methods have sometimes been used by Americans working with bryophytes, as, for example, by Norris (1964) in his Adirondack study, and by various students of bryophytic epiphytes. As pointed out above, epiphyte systems are especially dynamic, although characteristic groupings of species (communities in the sense used here) were found on particular tree species in this study.

Although the comparison of communities and of species populations along an elevation gradient is termed by myself and others direct gradient analysis, it must be kept in mind that elevation is in reality a complex gradient. Organisms do not respond to changes in elevation per se, but to a variety of environmental factors that change concomitant with elevation change. There is a striking change in the vegetation on Whiteface Mountain at about 2500 ft (760 m) where deciduous forest is replaced by spruce-fir forest. This change occurs at somewhat different elevations on different slopes of Whiteface and at somewhat lower elevations on Ampersand. In this study, no sharp differences in environmental conditions were observed at these elevations, and even the large-scale study of environment and vegetation on Whiteface (Scott and Holway, 1969) has been unable to document microclimatic changes at the transition elevations. Different environmental factors, such as growing seasons, maximum and minimum temperatures, annual precipitation, date of spring snowmelt, etc., could all be measured and graphed as the individual species populations were; each one probably follows a different pattern. At some elevation the "community" of these factors is such that the growth of red spruce and balsam fir is favored over that of most deciduous trees. (*Betula alleghaniensis*, *B. papyrifera* var. *cordifolia* and *Pyrus americana* do grow in the spruce-fir zone.) Environmental variables, such as exposure and prevailing winds, change with the direction of slope; thus, the community of factors favoring spruce-fir vegetation may occur at somewhat different elevations on different slopes.

In a recent study of the Green Mountains of Vermont, which are quite similar to the Adirondacks, Sicama (1974) concluded that the boundary between deciduous and coniferous (spruce-fir) forest was climatically, not edaphically controlled. His measurements showed a vertical climatic discontinuity accounting for the change in forest type. The two most important factors appeared to be the number of frost-free days per year and the frequency of the cloud base. The latter increased at about 790 m, which resulted in increased fog drip and hoarfrost, favoring coniferous over deciduous forest. The mean number of frost-free days decreased from 142 at 732 m to 103 at 914 m in de-

ciduous and spruce-fir forest, respectively. With a larger number of stations to record microclimatic data, these or similar factors could probably be shown to be important on Whiteface Mountain in the transition zone. The extent to which the transition is sharp or gradual will depend on the extent to which the changes in each of the important microclimatic factors occur at similar elevations.

The change from spruce-fir to arctic-alpine vegetation passes through a krummholz stage with stunted trees on some slopes occurring below the summit. Changes in environmental factors are more evident above timberline. Such changes within the arctic-alpine zone have been measured and related to the vegetation on Mt. Washington, New Hampshire, by Bliss (1963, 1969). On Whiteface, the effect of slope angle on vegetation has been measured by Nicholson and Scott (1969), who found it to be a major determinant of the altitude of timberline, and also of the diversity of vascular vegetation. These findings were confirmed in my study, but other microclimatic and topographic factors such as available water and habitat instability caused by rockslides also affect diversity of both bryophytes and vascular plants.

Duration of snow cover is another important factor that has not been examined systematically in the Adirondacks. Certain vascular plants and also bryophytes, e.g., *Polytrichum sexangulare* (formerly *P. norvegicum*) are known to be characteristics of areas of persistent snow cover. Winter and spring snow cover varies with location on Adirondack summits. I have been on the 5,000-foot summit of another Adirondack high peak, Mt. Algonquin, in March and observed sizable areas of arctic-alpine vegetation without any snow cover. On the other hand, on June 1, at least in some years, the 4400 ft (1340 m) quadrats are still under several feet of snow. The summit area of Whiteface, exposed to wind and high daytime insolation, was free of snow at that date. The high diversity found at 1340 m and the particularly high number of liverwort species are probably a result of increased moisture from the late snowmelt, and to the advantage of bryophytes over herbaceous vascular plants when the growing season is shortened by persistent snow cover. Bryophytes, unlike most vascular plants, can photosynthesize virtually as soon as uncovered; there is even evidence of photosynthesis of bryophytes under snow (Rastorfer, 1970; Longton, 1974). Photosynthesis at subzero (0°C) temperatures in the arctic has been recorded (Wilson, 1957) and may occur at these temperatures on Whiteface Mountain also. On the other hand, *Oxalis montana* comprised 84 percent of the total vascular ground flora at 1220 m, but is reduced to 22 percent in the quadrats with high bryophyte diversity at 1340 m.

At Kenrose Preserve the much shorter elevation range also proved important in terms of species diversity. In fact, elevation is the factor most highly correlated ($r = 0.69$) with bryophyte diversity (H'). Attempts to discover which aspects of elevation are important, that is, what actually happens to the bryophyte environment over the 130 m elevation gradient, were partially successful. Degrees of slope ($r = 0.46$) and pH ($r = 0.48$) were both significantly correlated with elevation and highly correlated with each other ($r = 0.79$). They are also each correlated with diversity (H'): $r = 0.60$ for degrees of slope and 0.45 for pH. Thus, elevation range at Kenrose is a complex factor including degrees of slope, pH, and probably differences in drainage as well, some combination of which are important for bryophyte diversity.

Bryophyte Diversity and Community Diversity

G. Evelyn Hutchinson's paper, 1959, "Homage to Santa Rosalia, or Why Are There So Many Kinds of Animals" was one of several that spurred the current interest in species diversity. The great majority of the research on diversity has involved animals or planktonic organisms in spite of the following, perhaps overlooked, statement in Hutchinson's paper:

Extraordinary diversity of the terrestrial fauna. . . is clearly due largely to the diversity provided by terrestrial plants.

He assumed that the three-fourths of a million insect species are in part a product of the diversity of terrestrial plant species and posed the really relevant question: "Why are there so many kinds of plants?"

Is the diversity of one segment of a community indicative of the overall diversity of the community, as suggested by Margalef (1963) and Johnson and Raven (1970)? This question can be asked regarding the various strata or taxonomic groups of the plant community.

My data suggest that one cannot obtain an index to the overall diversity of the plant community by sampling one segment. High bryophyte diversity is not correlated with high diversity of vascular plants whether H' or S is used as an index. Each stratum showed a different pattern of diversity with elevation in the Adirondacks. No correlation between diversity of vascular ground flora and that of bryophytes existed; shrub diversity showed an inverse correlation with that of bryophytes. The only direct correlation, in fact, was between diversity (H') of bryophytes and the number of tree species at Kenrose Preserve ($c = 0.58$). Even this relationship was not found elsewhere; that diversity of bryophytes is highest in the Adirondacks under

pure stands of balsam fir. In the arctic-alpine quadrats, the diversity of bryophytes is low, but that of another taxonomic group, the lichens, is high. Among vascular plants at that elevation, the shrub component of the communities has relatively high diversity, but the herbaceous vascular plant segment does not.

A closer relationship between the diversity of one segment of a community with another may exist when the segments have direct predatory-prey relationships, either between consumers, or between herbivore and host plant. High plant and high insect diversity are both found in the tropics, for example. MacArthur and MacArthur (1961) found that bird species diversity was more closely related to structural aspects of the vegetation than to the number of plant species present. Foliage height diversity (FHD) was the aspect of vegetation structure used, and this or similar measures of vegetation structure have since been found to be determinants of bird, lizards, and rodent diversity in other studies (MacArthur, Recher, and Cody, 1964; Pianka, 1966; Rosenzweig and Winakur, 1969). Tomoff (1974) found that FHD does not predict the number of bird species in desert scrub, but that a physiognomic coverage diversity based in part on the life forms of plants was a good predictor. Tomoff also found nest site specificity for desert birds in relation to plant species. Some other recent studies (Karr and Roth, 1971; Kricher, 1972; Cody, 1974) have discussed bird diversity in terms of vegetative structure, including beta (between-habitat) diversity of vegetation. The within-habitat studies have largely been of forest birds, usually secondary consumers and therefore not directly related in their food habits to specific plants. Prairie studies include herbivorous birds, but even these are rarely restricted to a particular species of plant. Studies of tropical fruit-eating birds might show closer bird and plant species diversity.

From an evolutionary point of view, there is no question that birds of one family can evolve in relation to plant species available, at least in the absence of competition from birds of other taxonomic groups. The niches of almost all the Galápagos finches (Lack, 1947) can ultimately be related to plant species on the islands.

The relationships between diversity of the insect and angiosperm sectors of the community can also be examined from an evolutionary viewpoint. The whole Cretaceous period was probably a time of extensive angiosperm and insect coevolution. Ehrlich and Raven (1964) cite coevolution of Papilionoidea (butterflies) and dicotyledons. Other examples of specific plant-insect coevolution, a subject initiated by Darwin, have been more recently given by Brower (1958) and Janzen (1969, 1970). Ehrlich and Raven (1964) conclude that the converse of Hutchinson's (1959) assumption may be true: phytophagous insects augment the diversity of

plants! Janzen (1970) supports a similar view in regard to seed-eating insects and tropical tree diversity. Two recent papers have discussed the relation between plant and insect diversity. Sharp, et al. (1974) found little relationship between butterfly and plant diversity in subalpine areas, but Murdoch, et al. (1972) working with Homoptera in fields, found high plant-insect correlation for both H' and J' . The butterflies were not as closely tied to particular plants as the Homoptera, some of which are host specific. Such specificity should increase the importance of plant diversity in relation to that of insects.

Bryophytes have few close ties with animals, apart from the species of the family Splachnaceae that live on dung, and whose spores are carried by Diptera. Several of these occur in the Adirondacks, though I have only found *Splachnum rubrum*; Splachnaceae are a more important part of bryophyte communities in the Arctic. Few herbivores eat bryophytes, although some animal unknown to me eats moss sporophytes, particularly those of *Polytrichum*, even on the summit of Whiteface. Tardigrades live on and apparently feed on bryophytes, and I have seen a variety of rotifers associated with bryophytes I have collected, but no one has yet made a diversity study of either of these groups of microscopic animals or their relation to bryophyte species.

Within the various sectors of the plant community, relationships are not as specific as between most bird or insect and plant species. Parasitic and semiparasitic plants (including angiosperms) are exceptions, as are those plants which produce chemicals inhibiting the growth of other plants. In this study a few species of epiphytic bryophytes were specific to their host trees, at least within the area studied. Higher epiphyte diversity was present on Ampersand Mountain in the mixed deciduous forest with many tree species than in the spruce-fir forest with fewer tree species. A pure beech or hemlock forest would have fewer epiphytic bryophyte species than a mixed hardwood-hemlock forest at the same elevation. Relationships between plant species in different strata are, in most cases, much less specific, usually involving environmental factors. The particular bryophytes found only in the oak-hickory forest at Kenrose Preserve are probably there in response to the same factors (low humidity? drier soil?) that favor the growth of these trees over maple or beech; the bryophytes are not there because of the particular tree species.

Especially harsh conditions, such as at the summit of Whiteface, may affect bryophytes and vascular plants similarly, resulting in a community consisting of species with similar tolerances in both of these strata. Species diversity is low in both these strata; relatively few species of either group are tolerant of summit conditions.

Species diversity relationships between segments of the plant community can also be looked at from an evolutionary viewpoint. The great majority of bryophytes in a temperate or tropical forest region are dependent on vascular plants for many aspects of their niches. Some bryophytes are obligate epiphytes on living trees; some liverworts are obligate epixyls on rotten logs (Barkman, 1958). In the tropics, in southern United States (Guerke, 1973) and even in the Pacific Northwest (Vitt, et al., 1973), some bryophytes are epiphyllic, that is, are epiphytes on living leaves, largely on evergreen angiosperms (or conifers in the north). In Puerto Rico, I have observed liverworts growing on ferns and aroids.

Even those forest bryophytes that are not so directly dependent on vascular plants as substrates are usually dependent on the shade and humidity provided by these plants. Although bryophytes are an ancient group and are not noted in general for rapid evolution, "explosive" evolution in some genera with many species is probably a relatively recent phenomenon. As such it is dependent on relationships with the vascular plant strata. I quote Schuster (1966) on this subject, with particular reference to liverworts:

... any explosive evolution in the Bryophyta came about only *after* evolution of a polytypic, complex, and rather complete cover of such groups as Pteridospermae, conifers, tree ferns, and Angiospermae, which, together with a rich ground and shrub flora (of ferns, lycopods, etc.), served to maintain humidity and reduce insolation. *Only after this* were conditions on land created that favored speciation in the Hepaticae. Indeed, I would go so far as to say that *today* conditions of so much greater diversity exist (compare tropical montane rain forests . . . and . . . cool subarctic rain forests . . .) than prior to the Mesozoic, so that extensive present-day microevolution (i.e., speciation) of Hepaticae and Musci is much more likely on a large scale than in most prior periods of their existence. [Italics Schuster's.]

Schuster goes on to give examples of recent "explosive" speciation in such families as Plagiogchiliaceae and points out that the majority of these species are arboreal and that their evolution "must postdate that of the dense, humid forests in which they have evolved most copiously." Thus, in the tropics and even in a temperate forest, there exists a very important relationship between the bryophyte diversity and that of vascular plants, in terms of bryo-communities. It is interesting to note that bryophytes have evolved to fill quite different niches provided by vascular plants, niches in which neither shade nor high humidity is present. In this study, species of *Frullania* were found on tree trunks in highly xerophytic conditions, i.e., in

open niches available to no other groups of plants except, perhaps, some lichen species. Evolution of special water-holding structures may have made the occupation of such niches by *Frullania* possible.

Two conclusions can be reached from the above discussion. First, one cannot assume that, by measuring the diversity of one segment of a community, whether birds, vascular plants, bryophytes, etc., the diversity of the community as a whole, or even of the plant or animal portion of it can be predicted. Significant correlations may exist, but more often they do not. Secondly, one segment of a community may be related, at least in an evolutionary sense, to the diversity of another or of several other segments. Present diversity relationships are complicated by other factors, such as competition both between and within segments of each trophic layer of a community.

Dominance-Diversity Curves and the Division of Niche Space

Dominance relationships among members of a community or one stratum of a community can be studied in several different ways. One method is by the calculation and comparison of evenness or "J" values. These have already been presented and compared, and are discussed further in the following section. Another method consists of plotting dominance diversity curves, as Whittaker (1965, 1970) has done for plant communities of the Great Smoky Mountains and elsewhere. These two methods have been used with my data, separately and in combination.

I have plotted dominance-diversity curves for bryophytes in the quadrats studied at Whiteface and at Kenrose Preserve, using relative cover values to rank the species in order of dominance. Whittaker's curves are plotted for vascular plants and are based on net annual production, although he has also used cover values and has stated (1965) that curves of similar form resulted for both types of values. The species are arranged (figs. 29 and 30) in order of their decreasing cover values, from highest to lowest cover value on the abscissa. The curve origins are spaced out for clarity; for example, the five species of the first Kenrose quadrat run from 1 to 5, but the 25 species of the last quadrat run from 25 to 49 (fig. 29). Relative cover value (or "abundance") is on a log scale.

Several different forms of curves result, some of them similar to those of Whittaker. In my quadrats of low diversity (low H' and low S) as in low diversity communities of Whittaker, straight lines of steep slope result. Whittaker pointed out that this type of curve approximates a geometric series. Translated into niche theory, such a series may be used as a model in which a dominant species preempts a certain percentage of

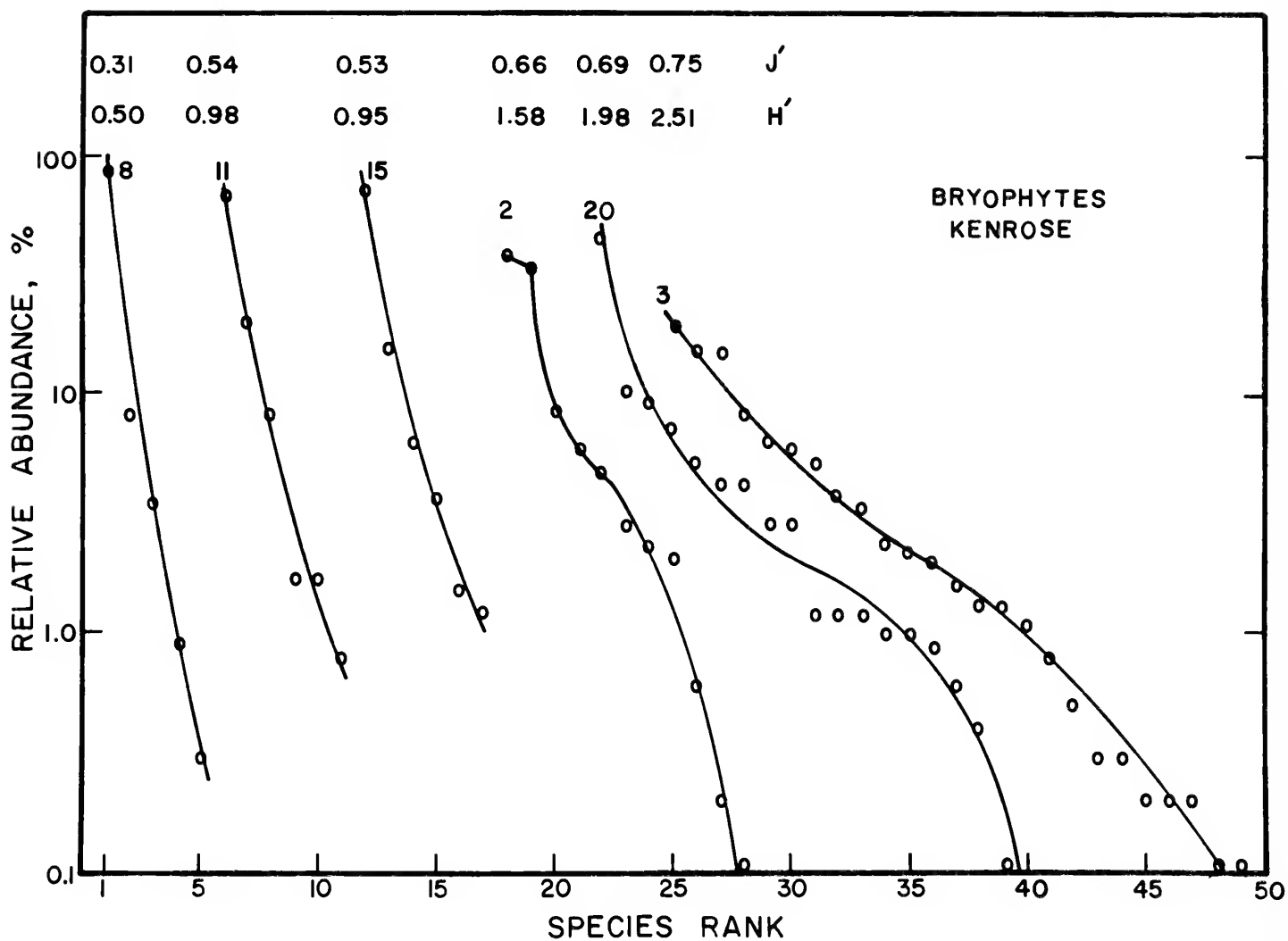


FIGURE 29 Dominance-diversity curves and J' and H' values for six quadrats at Kenrose Preserve (Nos. 8, 11, 15, 2, 20, and 3).

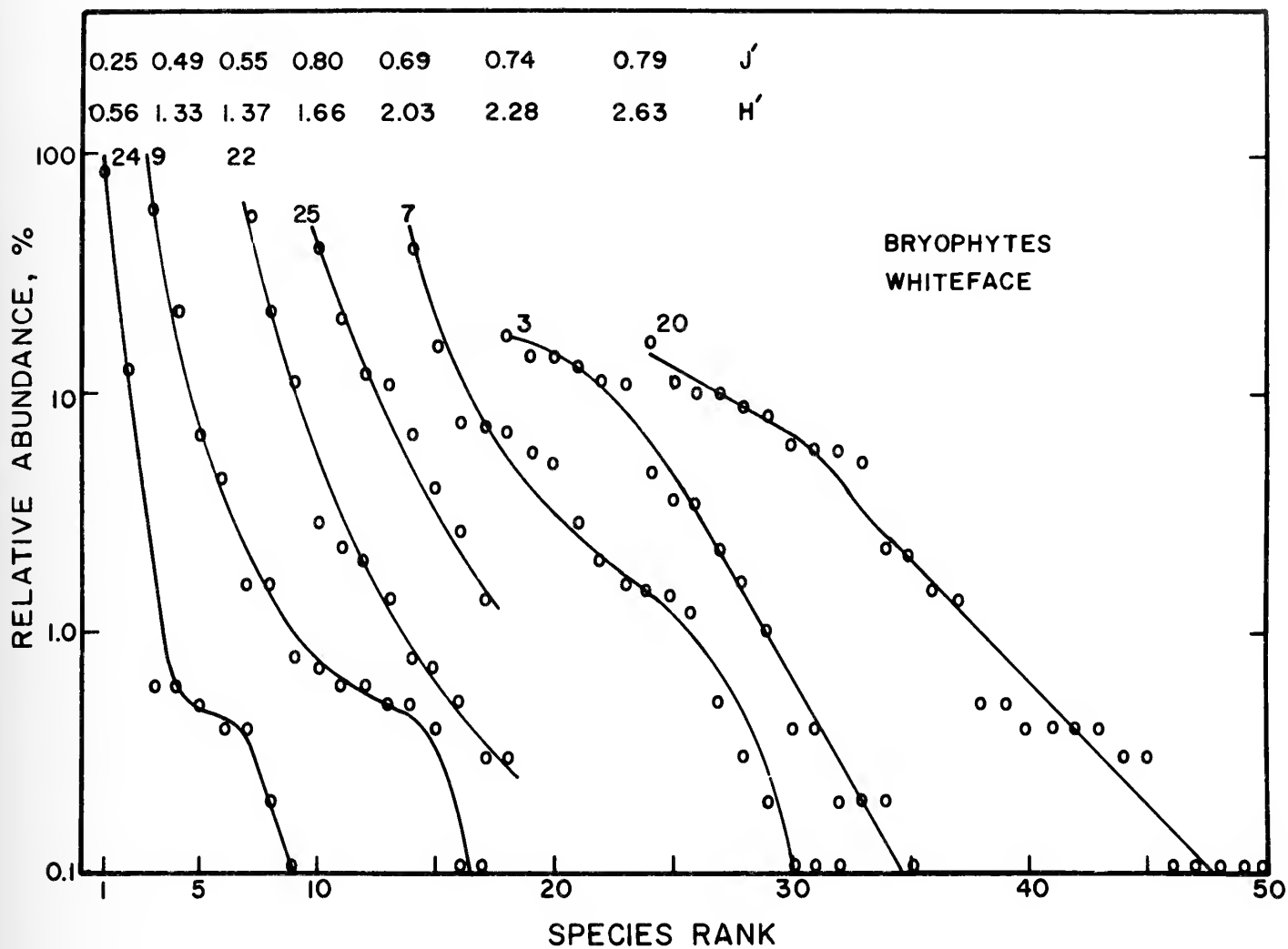


FIGURE 30 Dominance-diversity curves and J' and H' values for seven quadrats at Whiteface Mt. (Nos. 24, 9, 22, 25, 7, 3, and 20).

available niche space, c , approximated here by its percent cover, as follows:

The second ranked species occupies the same percentage of the remaining cover, $1-c$, generating the equation:

$$y = C(1-c)^{x-1}c$$

where y is the fraction of cover representing niche space for all species, C is total cover, and x is the species' rank.

None of the bryophyte curves shows a constant or nearly constant c , nor do those presented by Whittaker (1965, fig. 3). There is no particular reason to believe that each species should utilize the same proportion of niche space. Among the low diversity quadrats (8, 11, and 15 at Kenrose, and 24 and 25, both summit quadrats at Whiteface), considerable differences in division of niche space exist to an extent that this is actually reflected in dominance relationships. In quadrat 8 at Kenrose and 24 at Whiteface, one species has usurped the greatest extent of total bryophyte niche space, over 90 percent in quadrat 8. In these two quadrats either two or three species occupy over 99 percent of the niche space, resulting in very steep curves for this portion. Whiteface quadrats 24 and 9 (which has a large number of species but also a steep upper curve) have a relatively large number of species of low cover value. This pattern of dominance and diversity results in a sigmoid type of curve (fig. 30) not found among Whittaker's. Whittaker has omitted from his curves species of very low productivity, which may account for his steep lower curves, but it is also quite likely that bryophytes are able to divide remaining niche space more finely than can vascular plants.

I pointed out earlier that different dominance relationships are present even in low diversity quadrats in the same area, even when they have the same number of species as in quadrats 24 and 25 on the summit of Whiteface. The dominance-diversity curves for these quadrats (fig. 3) show these differences very strikingly. In 25, the initial curve is less steep with abundances of bryophyte species more evenly distributed than in 24, and there are no rare species. Different possibilities exist for the division of bryophyte niche space even under similar rigorous conditions.

Sigmoid curves similar to Whittaker's is, at least over the upper and middle portions, also resulted from my data. In terms of niche allocation, such curves (2 and 20, Kenrose, fig. 29, and 7, Whiteface, fig. 30) represent communities with more competing species, no one species usurping an especially large portion of niche space and with a large "middle class" utilizing similar portions of the niche space. In quadrat 2, Kenrose, there are two codominant species, a distribution also found by Whittaker.

Whittaker's communities of highest species diversity form similar sigmoid curves but of smaller slope. He used Preston's "lognormal" distribution as a model for these communities. This distribution consists of many species of intermediate abundance with fewer of greater and lesser abundance, approximating a normal curve when abundances are plotted on a log scale. The most diverse quadrats in my study area, represented here by 3, Kenrose (fig. 29) and 3 and 20, Whiteface (fig. 30) do not fit Preston's model. Preston's curve would be truncated at the upper end since no species in any of my high diversity quadrats has a relative abundance as high as 20 percent. The lower end of the curve would also differ because of the large number of bryophyte species of low relative abundance in these quadrats. These species can be seen on the dominance-diversity curves, which lack the steep drop at the end in contrast to Whittaker's curves for the high diversity communities in his studies.

As Whittaker himself noted (1965), there is no good reason to expect different strata of a community "subject to different environmental factors and modes of population limitation" to show parallel dominance-diversity relationships. When a plant community is extended to include the too often ignored bryophytes, differences in basic biology could be important. For example, Whittaker suggested that the lower portions of dominance-diversity curves may be affected by only partially adequate seed dispersal into the potential rare niche, leaving suitable niches empty, and presumably resulting in a steep lower curve. Bryophyte spore dispersal appears to me to be more successful in filling these niches. The ability of appropriate bryophytes to arrive at "rare" niches is often very striking, even when these niches are manmade. *Bryoerythrophyllum recurvirostrum* and *Encalypta procera* occur on a cement wall near the summit of Whiteface but were found nowhere else on the mountain (Reilly, 1964). Other species, such as *Tetraphis pellucida*, are nearly always found where their appropriate niches occur. This is true to such an extent that I am always surprised not to find *Tetraphis* on rotting conifer stumps of the appropriate stage of decay when I am out of the range of this species.

Furthermore, various types of open niches may each be filled by a number of different species of rare bryophytes, and this sort of opportunism, to be discussed below, probably also fills in the lower end of the dominance-diversity curve. Fitting any of these curves to mathematical models of niche space division may be premature. We know little about their multi-dimensional niche spaces, or their competitive relationships. Forman's (1964) experimental study of the physiological ecology of *Tetraphis pellucida* is probably the closest approach to elucidating the fundamental niche in Hutchinson's (1957) sense for any bryophyte

species. Other recent studies, though not experimental, have succeeded in measuring or identifying niche factors for bryophytes in particular habitats, for example, *Sphagnum* species in bogs (Vitt and Slack, 1975) and bryophytes on rotting logs (Mühle and LeBlanc, 1975). More such studies are needed before ecological theories of the division of niche space can be fully extended to bryophytes.

Finally, the shapes and slopes of dominance-diversity curves can be related to evenness (J') values as calculated from the Shannon function. These values, as well as those of H' are shown for each quadrat plotted in figures 29 and 30. For example, compare quadrat 3 at Whiteface with quadrats 7, Whiteface, and 20, Kenrose. All of these quadrats contain one or two dominant species and have the same evenness value ($J' = 0.69$). Quadrat 3 with six nearly equally dominant species at the top of the curve and therefore a higher evenness value (0.79), also has considerably higher diversity ($H' = 2.28$ as compared to 2.03 and 1.98 for the other two quadrats).

Although Whittaker stated that diversity is largely determined by the number of species in the middle portion of these curves, he was referring to diversity in terms of species richness (S). When highest diversity measured as H' is considered, it is obvious from the curves that H' is greatest when the species are evenly distributed throughout the curve; that is, over the upper as well as the middle portion. Such distribution results, of course, in the highest J' values. This pattern, and the resulting dominance-diversity curve, is an unusual one for bryophytes, at least in the forest habitats I have studied. High J' values were exceptional in this study; almost all were very low compared with Tramer's (1969) for birds or Pielou's (1966a, b) for herbaceous plants and shrubs.

Opportunism Among Bryophytes

Tramer (1969) has suggested that some groups of organisms tend to be "equilibrium" groups and to have their diversity (H') regulated largely by variation in species richness (S), while other groups are "opportunistic" and are more likely to have their species diversity regulated by variation in relative abundance or evenness (J'). Thus territorial birds living in stable, nonrigorous environments and having relatively stable population densities over time may be thought of as equilibrium species. Plankton, at the other extreme, live in unpredictable environments and a species' number may increase rapidly, but temporarily, when conditions are favorable.

All species in one group need not be entirely opportunistic or entirely equilibrium species; the Cape May warbler, a territorial bird, may be considered opportunistic because its population increases in response to the periodic abundance of spruce budworms. MacArthur (1960) defined the terms "opportunistic" and "equilibrium" and pointed out that photosynthetic organisms, including diatoms and early successional vascular plants, could also be placed in the opportunistic category.

According to Tramer (1969), groups of organisms with low and variable J' values can be considered opportunistic. He found high J' values (from 0.84 to 0.92), except for gregarious marsh birds. In addition, the J' values were stable; increased diversity (H') in his bird communities is closely correlated with increase in species richness (S). Thus, by his criteria, the species in these bird communities are not opportunistic. Sager and Hasler (1969), on the other hand, found lower J' values in their phytoplankton studies. Diversity (H') could not be predicted from species richness alone; the J' values were not stable. Therefore, according to Tramer's criteria, these phytoplankton species could be considered opportunistic, as MacArthur earlier suggested for diatoms.

By the same criteria, bryophytes, at least in certain habitats, can also be considered opportunistic. The J' values in my studies were low, as pointed out above, and also variable, at least in the Adirondacks. Out of all the quadrats studied, 29 percent had J' value under 0.6, 46 percent under 0.7, and 89 percent under 0.8. Most of the values ranged between 0.5 and 0.8, but values as low as 0.25 were found under rigorous summit conditions, as would have been predicted by Tramer. For bryophytes at Kenrose Preserve, entirely within deciduous forest biome, there was also great variation in J' , with values as low as 0.3. The majority of values are between 0.5 and 0.75, lower than those found by Pielou (1966a, b) for the herbaceous-shrub community in a Quebec study. Although species diversity (H') and species richness (S) are correlated for Kenrose bryophytes, there is great scatter of J' values at lower species numbers, indicating that even in deciduous forest in the more rigorous habitats (see Kenrose discussion) with low species richness, H' is not predictable from S . In the Adirondack study areas, J' is highly variable even in higher diversity quadrats; therefore, H' is not predictable from S even in these quadrats. In the summit quadrats on Whiteface, as pointed out above, quadrats with the same number of species sometimes have very different J' values.

Rigorous or unstable environments, e.g., the summit quadrats at Whiteface and the low elevation, seasonally mud-covered quadrats at Kenrose, are notable in these studies for low species richness and for low, though variable J' values as well. Some of the bryophytes species living in these environments prob-

ably are opportunistic in that they can persist and reproduce effectively in rapidly changing environments. Some are able to reestablish populations quickly after a landslide or mudflow. I do not mean to imply that all or most bryophyte species are opportunistic; most forest bryophytes probably are not. Other groups of organisms that consist largely of equilibrium species often contain some species or groups of species that are opportunistic in changing environments, such as the Cape May warbler (MacArthur, 1960), cited above, or black cherry (*Prunus serotina*) in disturbed oak forests in Wisconsin (Auclair and Cottam, 1971). For black cherry, the authors cited widespread dispersal, delayed seed germination, and flexible seedbed requirements as "opportunistic characteristics." Adaptation for successful establishment under nonequilibrium conditions seems to be as important as high reproductive rate for opportunistic species, at least among plants.

There is evidence besides that of J' or evenness values that some bryophytes are opportunistic, at least in certain environments. Schofield (1971), discussing bryophytes in the Arctic, wrote that "mosses are opportunistic in the high water table conditions, various taxa invading the shaded sites. . . yet others succeeding in the open well-illuminated areas." He also pointed out a number of species that were able to invade unoccupied sites such as rocks in streams and bare silt, and cited a study of Whitmire (1965) on the early establishment of opportunistic species on dung, followed, as pH becomes more like that of the surrounding bog, by common bog species, perhaps the equilibrium species of this environment. Other arctic bryophytes, e.g., *Bryum wrightii* (Steere and Murray, 1974), also appear to be opportunists, appearing in such disturbed habitats as lemming runways.

Crum (1966) stated that "open disturbed situations are usually quickly occupied by species of broad ecological tolerances and short life cycles or both," although he does not believe disturbed sites to be suitable to the majority of mosses. Many mosses, such as *Pleurozium schreberi* in balsam fir forest in the Adirondacks, appear to be occupants of stable sites and represent the "equilibrium species" among bryophytes.

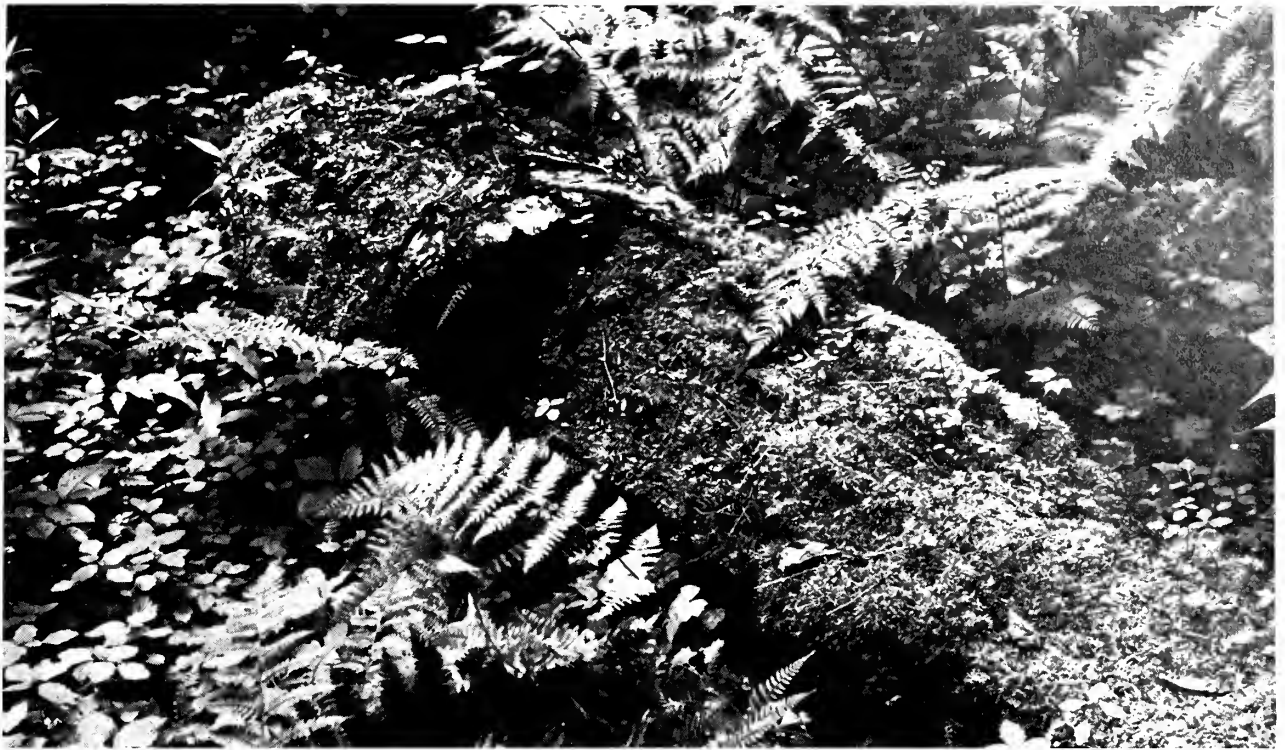
Schuster (1966) described the exploitation by bryophytes, and especially by liverworts, of sites in the tropics not occupied by other plants, such as the surfaces of living leaves and twigs (also of interest in connection with the high species diversity of tropical liverworts). The exploitation of the twig habitat is also illustrated by Herzog (in Gams, 1932) with a photograph of a small twig of *Berberis* in Bolivia bearing five different bryophyte species. The epiphyllous habitat also is a short-lived, unstable one. Although the leaves are usually evergreen and persist long enough for the

bryophyte to reproduce, sexually or asexually, the population perishes when the leaf falls. Propagules are easily and quickly dispersed to other leaves, as is characteristic of opportunistic species.

Outside the tropics, many liverworts are equally limited to temporary or extreme habitats such as decaying logs or snowfield margins, or, as in this study, the bark of trees. Schuster (1966) considered liverworts, and perhaps bryophytes as a group, to a large extent opportunistic; "the less mature and more extreme [the environment] the more diverse and conspicuous the bryophyte flora." He also cited some rare experimental evidence: Griggs (1934, 1935) found two liverwort species (both of Adirondack genera) that could grow and reproduce on nitrogen-free volcanic ash where other plants could not. When nitrogen was added, algae and moss protomema crowded the liverworts out. Opportunism and lack of competitive ability under conditions of higher productivity and stability appear to be correlated for certain species. This correlation may be found in liverworts as a group more often than in mosses, though it is not characteristic of all liverworts, e.g., *Bazzania trilobata*, in the Adirondacks.

Another somewhat different type of opportunism has to do with stochastic or chance factors and is related to the last question I want to consider here: the relationship for bryophytes of species diversity, niche space, and the Gaussian principle. Schuster discussed elsewhere (1957) the composition of pioneer bryophyte communities growing as epiphytes on *Thuja*, and in another example, on decorticated logs. On *Thuja* he found 11 different combinations of liverwort species alone. He stated that these species were all ecologically very similar and concluded that the most important factor in the determination of groupings was chance; that is, which species happened to arrive first. In the decorticated log habitat, he found a total of 25 ecologically similar "candidates" for invasion of this environment. He concluded that "environment plus chance plus time governed what species shall undergo ecesis [successful establishment] . . . If a species has a slight advantage in time . . . it tends to form large, pure patches, due to extraordinary high reproductive potential." The latter is due largely to asexual reproductive structures, another frequent characteristic of opportunistic plant species.

Schuster, also noted the occurrence on some of these logs of a great number of ecologically similar species that "undergo ecesis on the same site at the same time." The heterogeneous community formed "results from gregariousness of sociability of many species of Hepaticae (and mosses)." This same gregariousness, the presence of many different species occupying one small area of apparently uniform environment, has been noted by many bryologists. Steere (1951) noted it on Cornwallis Island in the Arctic.



Bryophyte community of a rotten log, hemlock-hardwood forest, Ampersand Mountain, containing 15 or more species.



(photo by N. C. Slack)

Diverse bryophyte community overhanging rock face, Whiteface Mountain.

Schofield (1971) wrote that "the apparent lack of competition among a diversity of taxa of bryophytes in a small area is shown by the universal occurrence of this phenomenon in the arctic." It is also a common phenomenon in the deciduous and spruce-fir forests I have studied, particularly on logs, both decorticated and in earlier stages of decay. I have frequently found as many as fifteen species of bryophytes on one log, with little apparent differentiation of microhabitat for the majority of them, though a few are characteristic of damper undersides.

Do Gaussian principles of "competitive exclusion" really hold for bryophytes in such habitats? In many habitats the bryophytes found in such assemblages belong to the same genera, *Mnium*, *Brachythecium*, and *Hypnum*, for example, on logs in early stages of decay, and *Cephalozia* on decorticated logs. Must we believe Slobodkin (1961) that the "portions of the fundamental niches of two [ten?] species. . . that are found to coexist are not identical"? Or, "if they seem to be identical the study is incomplete"? Perhaps we can use Slobodkin's phrase "persist indefinitely" to wriggle out of this dilemma. These apparently coexisting species obviously do not persist indefinitely; their habitats are temporary. When the log decays completely, as when the leaf with its epiphyllous bryophytes falls, the species coexist no longer. These are in a sense fugitive species (Hutchinson, 1965) which when displaced, in this case not by a competitor but by the disappearance of their habitat, are mobile enough in terms of sexual or vegetative propagules to establish themselves on new open sites (e.g., another newly fallen log in the Adirondack forest). Hutchinson pointed out that a similar idea has been advanced by Skellam for annual plants, which must find a new site each year. Perhaps they, too, thus avoid the problems of competitive exclusion.

Even with a long-persistent rotting log, there is another way of avoiding Gaussian fate, suggested both by Hutchinson (1964) and by Levin (1970). In Hutchinson's terms, "If two species were almost equally efficient over a wide range of environmental variables, competitive exclusion would be a slow process." It seems to me that with nearly equal efficiency in the rotten log habitat, exclusion could be slow enough even without the random environment suggested by these authors.

In conclusion, I believe that the solution to this problem of coexistence of closely related species of bryophytes is very important to the understanding of bryophyte diversity and its importance in a plant community. Bryophyte diversity, where measured as S or H' (or very likely by any other method) increases as the number of suitable bryophyte habitats increases, whether this increase consists of spatial heterogeneity in terms of logs, rocks, etc., within one quadrat, or

consists of a large elevation range with resulting vegetation types. Furthermore, diversity is increased where a large variety of bryophytes apparently coexist in any one such suitable habitat, whether it is a moss (and liverwort) covered log in the Adirondack spruce-fir zone, or an epiphytic site in a montane tropical rain forest. It is surely true that "the study is incomplete" and we may yet find differences between realized niches of all the apparently coexisting bryophytes. We may as likely find that bryophytes are in large part opportunistic species, and that their primary role and in their contribution to the species diversity of plant communities is in their coexistence, not indefinitely but persistently, in ultimately temporary habitats, and in their ability to exploit a variety of habitats not suitable to other sectors of the plant community.

These intensive studies of bryophyte ecology in New York State forests have identified some problems of bryophyte species diversity and community structure, and have provided data for some tentative answers. Many more studies are needed of bryophytes in forest habitats of other regions, and in other types of habitats before we can gain a better understanding of these problems.

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APPENDIX A

Bryophytes Found in Adirondack Quadrats (Whiteface and Ampersand Mts.)

Mosses

Amblystegium juratzkanum Schimp.
Amblystegium serpens (Hedw.) B.S.G.
Amblystegium varium (Hedw.) Lindb.
Andreaea rupestris Hedw.
Anomodon rugellii (C. Müll.) Keissl.
Atrichum angustatum (Brid.) B.S.G.
Atrichum undulatum (Hedw.) P. Beauv.
Brachythecium acuminatum (Hedw.) Aust.
Brachythecium curtum (Lindb.) Limpr.
Brachythecium oxycladon (Brid.) Jaeg. and Sauerb.
Brachythecium populeum (Hedw.) B.S.G.
Brachythecium reflexum (Starke ex Web. and Mohr.)
 B.S.G.
Brachythecium rutabulum (Hedw.) B.S.G.
Brachythecium salebrosum (Web. and Mohr.) B.S.G.
Brachythecium velutinum (Hedw.) B.S.G.
Brotherella recurvans (Michx.) Fleisch.
Bryum capillare Hedw.
Callicladium haldanianum (Grev.) Crum
Campylium chrysophyllum (Brid.) J. Lange
Campylium hispidulum (Brid.) Mitt.
Dicranella heteromalla (Hedw.) Schimp.
Dicranum flagellare Hedw.
Dicranum fulvum Hook.
Dicranum fuscescens Turn.
Dicranum montanum Hedw.
Dicranum polysetum Sw.
Dicranum scoparium Hedw.
Dicranum undulatum Brid.
Dicranum viride (Sull. and Lesq. ex Sull.) Lindb.
Drepanocladus uncinatus (Hedw.) Warnst.
Encalypta procera Bruch.
Eurhynchium pulchellum (Hedw.) Jenn.
Fissidens osmundoides Hedw.
Grimmia affinis Hornsch.
Grimmia apocarpa Hedw.
Grimmia donniana Smith
Hedwigia ciliata (Hedw.)
Herzogiella striatella (Brid.) Iwats.
Herzogiella turfacea (Lindb.) Iwats.
Hylocomium splendens (Hedw.) B.S.G.
Hypnum imponens Hedw.
Hypnum lindbergii Mitt.
Hypnum pallescens (Hedw.) P. Beauv.
Isopterygium distichaceum (Mitt.) Jaeg. and Sauerb.
Leucobryum glaucum (Hedw.) Angstr. ex Fr.
Mnium ciliare (C. Muell.) Schimp.
Mnium hymenophyloides Heub.
Mnium punctatum Hedw.
Mnium spinulosum B.S.G.

Neckera pennata Hedw.
Oncophorus wahlenbergii Brid.
Paraleucobryum longifolium (Hedw.) Loeske
Plagiothecium denticulatum Hedw. B.S.G.
Plagiothecium laetum B.S.G.
Platydictya subtile (Hedw.) Crum
Platygytium repens (Brid.) Mitt.
Pleurozium schreberi (Brid.) Mitt.
Pogonatum alpinum (Hedw.) Roehl.
Pogonatum dentatum (Brid.) Brid.
Pohlia elongata Hedw.
Pohlia nutans (Hedw.) Lindb.
Polytrichum juniperinum Hedw.
Polytrichum ohioense Ren. and Card.
Polytrichum piliferum Hedw.
Polytrichum strictum Brid.
Ptilium crista-castrensis (Hedw.) De Not.
Rhacomitrium fasciculare (Hedw.) Brid.
Rhacomitrium heterostrichum (Hedw.) v. sudeticum
 (Funck) Dix. ex Bauer
Rhodobryum roseum (Hedw.) Limpr.
Rhynchostegium serrulatum (Hedw.) Jaeg. and Sauerb.
Sphagnum capillaceum (Weiss.) Schrank
Sphagnum girgensohnii Russ.
Sphagnum quinquefarium (Lindb. ex Braighw.)
 Warnst.
Taxiphyllum deplanatum (Bruch and Schimp. ex Sull.)
Tetraphis pellucida Hedw.
Thuidium delicatulum (Hedw.) B.S.G.
Thuidium recognitum (Hedw.) Lindb.
Tortella humilis Hedw. Jenn.
Tortella tortuosa (Hedw.) Limpr.
Ulota crispa (Hedw.) Brid.
Ulota hutchinsiae (Sm.) Hamm.
Ulota coarctata (P.-Beauv.) Hamm.

Liverworts

Anastrophyllum michauxii (Huds.) Buch
Anastrophyllum minutum (Cr.) Schuster
Barbilophozia barbata (Schmid.) Dumort.
Bazzania trilobata (L.) Gray
Blepharostoma trichophyllum (L.) Dumort.
Calopogeia fissa (L.) Raddi
Calopogeia muelleriana (Schiffn.) K. Muller
Cephalozia bicuspidata (L.) Dumort.
Cephalozia laciniata (Jack) Spruce
Cephalozia media Lindb.
Cephaloziella hampiana (Nees) Schiffn.

Frullania asagrayana Mont.
Frullania eboracensis Gottsche
Gymnocolea inflata (Huds.) Dumort.
Jamesoniella autumnalis (D.C.) Steph.
Lepidozia reptans (L.) Dumort.
Lophocolea heterophylla (Schrod.) Dumort.
Lophozia attenuata (Mart.) Dumort.
Lophozia ventricosa (Dicks.) Dumort.
Marsupella emarginata (Ehr.) Dumort.
Mylia taylori (Hook.) Gray
Nowellia curvifolia (Dicks.) Mitt.
Pellia epiphylla (L.) Corda
Ptilidium ciliare (L.) Nees
Ptilidium pulcherrimum (Web.) Hampe
Radula complanata Dumort.
Radula obconica Sull.
Scapania nemorosa (L.) Dumort.
Tritomaria exectiformis (Breidl.) Schiffn.

APPENDIX B

Bryophytes Found in Quadrats at Kenrose

Preserve

Mosses

Amblystegium serpens (Hedw.) B.S.G.
Amblystegium varium (Hedw.) B.S.G.
Anomodon attenuatus (Hedw.) Hueb.
Atrichum undulatum (Hedw.) P.-Beauv.
Brachythecium acuminatum (Hedw.) Aust.
Brachythecium oxycladon (Brid.) Jaeg. and Sauerb.
Brachythecium populeum (Hedw.) B.S.G.
Brachythecium reflexum (Starke ex Web. and Mohr.)
 B.S.G.
Brachythecium salebrosum (Web. and Mohr.) B.S.G.
Brachythecium velutinum (Hedw.) B.S.G.
Brotherella recurvans (Michx.) Fleisch.
Bryum capillare Hedw.
Callicladium haldanianum (Grev.) Crum
Campylium chrysophyllum (Brid.) J. Lange
Campylium hispidulum (Brid.) Mitt.
Climacium americanum Brid.
Dicranella heteromalla (Hedw.) Schimp.
Dicranum flagellare Hedw.
Dicranum fulvum Hook.
Dicranum fuscescens Turn.
Dicranum montanum Hedw.
Dicranum scoparium Hedw.
Dicranum viride (Sill. and Lesq. ex Sull.) Lindb.
Ditrichum pallidum (Hedw.) Hampe
Eurhynchium hians (Hedw.) Sande Lac.
Eurhynchium pulchellum (Hedw.) Jenn.
Fissidens osmundoides Hedw.

Fissidens taxifolius Hedw.
Fissidens viridulus (Sw.) Wahlenb.
Grimmia apocarpa Hedw.
Haplocladium virginianum (Brid.) Broth.
Hedwigia ciliata (Hedw.) P.-Beauv.
Homomallium adnatum (Hedw.) Broth.
Hypnum cupressiforme Hedw.
Hypnum imponens Hedw.
Hypnum lindbergii Mitt.
Hypnum pallescens (Hedw.) Broth.
Leskeella nervosa (Brid.) Loeske
Leucobryum glaucum (Hedw.) Angstr. ex Fr.
Mnium ciliare (C. Muell.) Schimp.
Mnium cuspidatum Hedw.
Mnium punctatum Hedw.
Physcomitrium pyriforme (Hedw.) Hampe
Plagiothecium denticulatum (Hedw.) B.S.G.
Plagiothecium laetum B.S.G.
Platydictya confervoides (Brid.) Crum
Platygyrium repens (Brid.) B.S.G.
Pleurozium schreberi (Brid.) Mitt.
Pohlia nutans (Hedw.) Lindb.
Polytrichum commune Hedw.
Polytrichum juniperinum Hedw.
Polytrichum ohioense Ren. and Card.
Polytrichum piliferum Hedw.
Racomitrium heterostichum Hedw.
Rhynchostegium serrulatum (Hedw.) Jaeg. and Sauerb.
Rhytidiadelphus triquetris (Hedw.) Lindb.
Tetraphis pellucida Hedw.
Thuidium delicatulum (Hedw.) B.S.G.
Thuidium recognitum (Hedw.) Lindb.
Ulota crispa (Hedw.) Brid.
Weissia controversa Hedw.

Liverworts

Bazzania trilobata (L.) Gray
Cephalozia bicuspidata (L.) Dumort.
Cololejeunia biddlecomiae (Aust.) Evs.
Jamesoniella autumnalis (D.C.) Steph.
Lophocolea heterophylla (Schrad.) Dumort.
Pellia epiphylla (L.) Corda
Plagiochila asplenioides (L.) Dumort.
Ptilidium pulcherrimum (Web.) Hampe
Radula complanata (L.) Dumort.

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